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Life History of Cobia, *Rachycentron canadum* (Osteichthyes: Rachycentridae), in North Carolina Waters

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ABSTRACT.—Cobia ($n = 416$) were collected primarily along the central North Carolina Atlantic coast from recreational anglers between 1983 and 1994. Males ($n = 174$) ranged up to 136-cm fork length (FL) and 32.0 kg, and females ($n = 182$) up to 142-cm FL and 32.2 kg. Most cobia greater than 100-cm FL were females. Ages of cobia (to age 14) were estimated by counting opaque zones on cross-sectioned sagittal otoliths. Von Bertalanffy growth parameter (k) estimates were 0.37 for males and 0.24 for females. Adult cobia occurred in major sounds and coastal Atlantic waters of North Carolina from May through July, and in nearshore oceanic waters through fall. Cobia may overwinter between Cape Fear and Cape Canaveral at depths of 30–75 m. Cobia fed chiefly on demersal crustaceans and fishes in the study area. Cobia may be one of the few teleosts that regularly consumed small elasmobranchs. Male cobia were sexually mature at 60–65-cm FL (age 2), and females at 80-cm FL (age 2). Cobia spawned May through July along the North Carolina coast, and ocean waters adjacent major coastal inlets were probable sites for cobia spawning activity.

Cobia, *Rachycentron canadum*, a large, coastal fish of the monotypic family Rachycentridae, has a cosmopolitan distribution in tropical to warm temperate seas, except for the eastern Pacific Ocean (Briggs 1960, Shaffer and Nakamura 1989). Cobia occur during summer in the United States coastal waters of the northern Gulf of Mexico and along the Eastern Seaboard from the Florida Keys north to Cape Cod (McClane 1965), although they are uncommon north of Chesapeake Bay (personal observations). Cobia migrate north along the Atlantic coast from northern Florida to the Carolinas, and then into Chesapeake Bay (McClane 1965, Shaffer and Nakamura 1989) during spring and summer. By late spring and early summer cobia enter polyhaline to mesohaline areas of major coastal bays, sounds and river systems in the Carolinas and Virginia (Musick 1972, Moore et al. 1980, Schwartz et al. 1981). Lone fish or “pods” of several cobia often hover in the shadow of near-surface objects, such as buoys, boats, sharks, and

rays (Joseph et al. 1964, McClane 1965, Shaffer and Nakamura 1989). Their size, commonly exceeding 23 kg (McClane 1965), and nearshore residence during spring through summer, make them a favorite of coastal recreational fishermen. Recent estimates (1991) place recreational cobia landings along the United States south Atlantic coast (292,600 kg) at five times that of commercial landings (58,000 kg) (Isley 1992).

To date, Richards (1967) conducted the most comprehensive life history study of cobia on the Atlantic coast of the United States, collecting specimens during the mid-1960s in lower Chesapeake Bay. Various facets of cobia biology have been examined, including feeding habits (Knapp 1951, Darracott 1977), reproduction (Biesiot et al. 1994), spawning areas and season (Joseph et al. 1964), movements and growth (Richards 1977, Franks 1995), rearing eggs and larvae (Hassler and Rainville 1975), and egg and larval distributions (Ditty and Shaw 1992). Recent mitochondrial DNA analyses (Hrincevich and Biesiot 1994) suggested that cobia from the northern Gulf of Mexico and the south Atlantic coast of the United States should be considered a unit stock. Shaffer and Nakamura (1989) compiled a biological synopsis of the species.

My interest in cobia stems from (1) a perceived increase in fishing effort for the species along the North Carolina coast during the 1980s, including a directed charter boat fishery for cobia at Ocracoke Inlet and the establishment of a cobia fishing tournament in Carteret County, and (2) the lack of contemporary fishery statistics on which to base cobia stock assessments (Gulf of Mexico and South Atlantic Fishery Management Councils 1985, Isley 1989). Objectives were to elucidate various aspects of cobia life history in North Carolina waters, in particular, age and size composition of the recreational catch, distribution, feeding habits, and reproduction.

MATERIALS AND METHODS

Recreational fishermen in the Morehead City-Beaufort area (Carteret County) of the central North Carolina coast (Fig. 1) were the major sources of specimens from 1983 to 1994. Beginning in June 1987 and each spring thereafter, fish were processed at a local cobia tournament. Additionally, during 1989–92 charter boat captains and tackle shop proprietors at Ocracoke Island and Hatteras, North Carolina, provided frozen cobia carcasses, individually labeled with date, location of capture, and whole (round) mass; for most of these specimens the head, axial skeleton and viscera were intact. Carcasses were returned to the laboratory biweekly for processing. Additional specimens came from pound nets and haul seines in Pamlico Sound near Cape Hatteras, ocean research

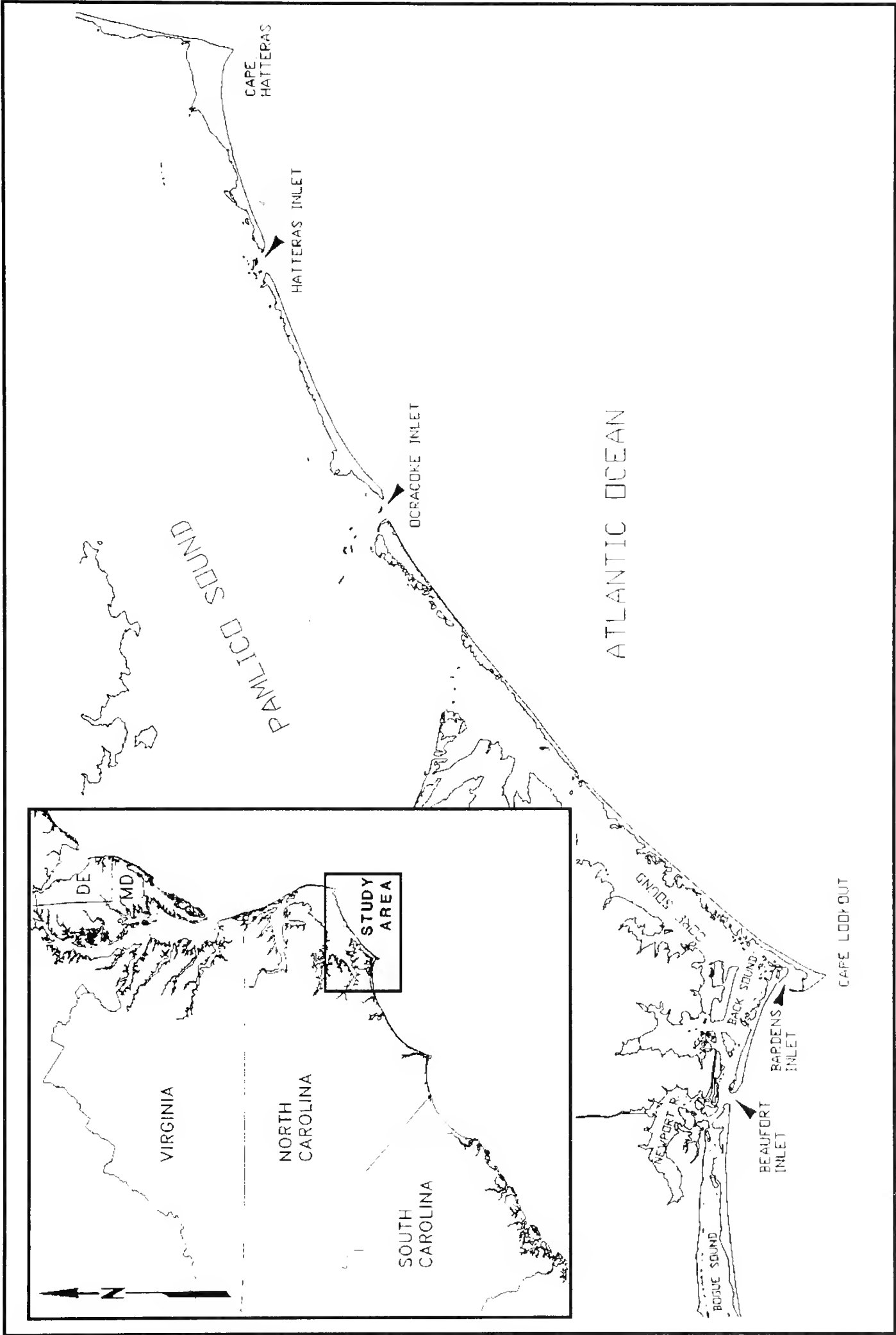


Fig. 1. Major sampling sites (arrows) for cobia along the North Carolina coast, 1983-94.

cruises between Cape Lookout, North Carolina, and northern Florida, research trawls in lower Chesapeake Bay, and port agents in South Carolina and northeast Florida.

Whole cobia were weighed to the nearest 0.1 kg. Carcasses and whole cobia were measured for total (TL) and fork length (FL) in centimeters and sexed. Gonads were staged for maturity based on criteria in Waltz et al. (1979), then excised and weighed to the nearest gram. Subsamples of fresh gonadal tissue from 99 cobia were preserved in 10% buffered formalin, and later sectioned by standard histological techniques (Humason 1972) to verify maturity staging in the field. A gonadosomatic index (*gsi*) was computed for sexually mature specimens, whereby $gsi = (\text{gonad mass/body mass}) \times 100$. Axial skeletons were missing from some frozen specimens, as catches were “steaked” versus filleted. Fork lengths for fish lacking an axial skeleton were estimated by calculating a regression of FL on intraorbital distance (measured with a caliper in mm) from whole fish (Table 1). Fork length was then assigned to carcasses based on this regression.

Table 1. Mass-length (ln) and length-length regression equations for cobia from North Carolina and adjacent waters, 1983-94.

Variables ^a	Sex ^b	<i>n</i>	Equation	R ²	Range
W-FL	♂	86	$\log W = 3.4 \log FL - 13.3$	0.972	0.5–32.0 kg
	♀	94	$\log W = 3.2 \log FL - 12.3$	0.949	0.7–32.2 kg
	♂ + ♀ + I	194	$\log W = 3.4 \log FL - 13.0$	0.987	0.5–32.2 kg
TL-FL	♂	105	$TL = 1.1 FL - 1.1$	0.989	39–136 cm FL
	♀	97	$TL = 1.1 FL + 0.7$	0.993	44–142 cm FL
	♂ + ♀ + I	217	$TL = 1.1 FL - 0.9$	0.995	39–142 cm FL
FL-IO	♂	75	$FL = 0.8 IO + 17.3$	0.929	39–136 cm FL
	♀	65	$FL = 0.8 IO + 18.5$	0.956	44–142 cm FL

^a W = fish mass in kg, IO = intraorbital distance in mm, FL and TL in cm.

^b I = undifferentiated specimens.

Stomachs were examined and the contents were preserved in 10% formalin and later transferred to 50% isopropanol. Bait or chum (fish that had obviously been sliced or cut by anglers, mostly Atlantic menhaden, *Brevoortia tyrannus*, pinfish, *Lagodon rhomboides*, and various sciaenids) occurred in 37 stomachs; these items were eliminated from any analyses, as were 15 stomachs where bait or chum was the only food item

present. Represented food items were drained, identified, counted, and weighed to the nearest gram.

Importance of each prey item to the cobia diet was based on an index of relative importance (*iri*; Pinkas et al. 1971). Percent frequency of occurrence for each item in non-empty stomachs (*f*), percent total number of prey items (*n*), and percent total mass of prey items (*w*) were calculated. The original *iri* formula was modified to use the mass of a prey item instead of volume, ($iri = f(n+w)$). The results were examined for areal differences in diet (Beaufort Inlet and vicinity, Ocracoke and Hatteras inlets and vicinity, and offshore oceanic waters). To determine changes in cobia food habits with growth, specimens with food items were partitioned into arbitrary size classes (<4.5, 4.5–9.0, and >9.0 kg), and prey items were grouped into four categories, that is, shrimps, crabs, teleost fishes, and elasmobranch fishes. Percent *iri*'s were calculated as a percent of total *iri* within each cobia size class.

Acetate impressions of cobia scales were difficult to interpret, therefore, sagittal otoliths of cobia were used to estimate specimen age. Sagittae of cobia were removed, washed in distilled water, and stored dry in individually labeled envelopes. Sagittae were embedded in 14x6x3-mm epoxy molds. Casts were affixed to a microscope slide with a drop of cyanoacrylate glue, then clamped to the arm of a circular low-speed saw. A 0.5-mm transverse section was made through the sagittal focus using a diamond-edge circular blade. The resulting wafer was permanently mounted to a microscope slide with a fixative.

Sagittal sections were viewed on a dissecting microscope (16x) with transmitted, polarized light. Cross-sectioned sagittae had an opaque central core, followed by alternating translucent and opaque zones (Fig. 2). Although marginal increment analyses were precluded because specimens were unavailable throughout the year, most sagittae had an opaque edge, or an opaque zone in close proximity to the sagittal edge. Moreover, research in the northern Gulf of Mexico (Franks et al. 1991, Thompson et al. 1991) confirmed the validity of the formation of one translucent and one opaque zone on cobia sagittae each year. Thus, I assumed that one translucent and one opaque zone was deposited each year, and that opaque zones could be used to estimate cobia ages.

Opaque zones along the ventral medial axis were counted as apparent annuli; estimated fish ages were based on opaque zone counts. I used the SAS NLIN procedure with the Marquardt option (SAS Institute, Inc. 1987) to estimate von Bertalanffy growth parameters based on individual fork lengths. Lengths referred to in the text are fork lengths.

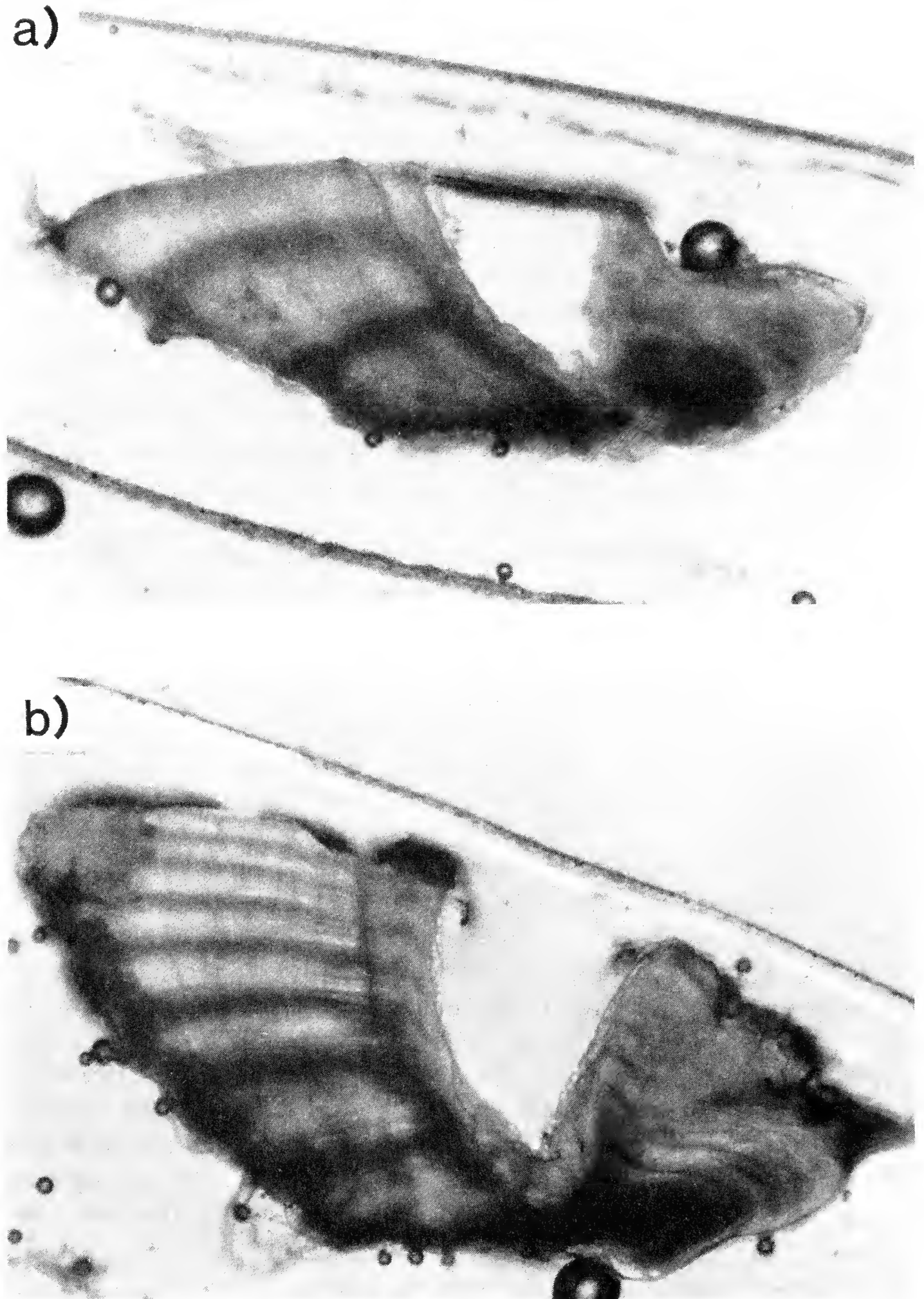


Fig. 2. Cross-sections (0.5 mm thick) of cobia sagittae: a) sagitta from age 3 fish (89 cm FL male, 18x magnification), b) sagitta from age 8 fish (125 cm FL female, 18x magnification). Note that spheres are artifacts of fixative.

RESULTS

SIZE AND AGE COMPOSITION

Four hundred sixteen cobia were collected. Most ($n = 366$) were acquired from recreational hook-and-line fishermen, while others came from trawls ($n = 34$), gill nets ($n = 7$), pound nets ($n = 4$), stop nets ($n = 2$), long hauls ($n = 2$), and purse seine ($n = 1$). A majority ($n = 356$) of the specimens came from North Carolina waters, mostly from inlet areas. A few specimens were from the Virginia portion of Chesapeake Bay ($n = 17$), and others were collected by port agents in South Carolina ($n = 11$), and northeast Florida ($n = 15$). Research trawls (75-ft high-rise mongoose net) from Daytona Beach, Florida, to Cape Lookout, North Carolina captured 17 specimens at ocean stations in depths 7–17 m.

Using pooled data from all gear types, 174 male cobia ranged from 39 to 136 cm and 0.47 to 32.0 kg, and 182 females ranged from 44 to 142 cm and 0.66 to 32.2 kg (Fig. 3). Only 27 of 152 (17.8%) males, taken by hook-and-line, measured greater than 100 cm; conversely 91 of 174 (52.3%) of the females caught by the same gear were greater than 100 cm (Fig. 3).

North Carolina enacted bag (2 fish/angler/day) and minimum size limits (33 inches [84 cm] FL) for cobia in 1991, thus bringing the state in line with corresponding cobia regulations in other south Atlantic states and the Federal Fisheries Conservation Zone (3–200 miles from shore). Between 1983 and 1990, 261 cobia caught by hook-and-line were examined, and 65 (24.9%) were less than 84 cm. Between 1991 and 1994, only five (5.3%) of 93 fish caught by hook-and-line were less than 84 cm, and four of these were 82–83 cm.

Sectioned sagittae from 326 specimens were examined for opaque zone counts (Fig. 2). Mean observed fork length of cobia increased with opaque zone count (Table 2). Otoliths with no opaque zones distal to the sagittal core presumably came from young-of-the-year cobia that averaged 31-cm ($n = 17$, range = 21–46-cm). Age 1 cobia, or those with one opaque zone distal to the core, averaged 51 cm ($n = 9$, range = 39–64-cm). Mean length of females was larger than mean length for males at a given estimated age (Table 2). Maximum estimated age was 14 for males, and 13 for females. The von Bertalanffy growth coefficient, k , was greater for males than females, although mean asymptotic size was larger for females (Table 3).

SEASONALITY AND DISTRIBUTION

Initial catches of cobia by North Carolina anglers usually occurred in March or April 50–65 km offshore over rocky outcroppings and

Table 2. Sample size (*n*), fork length range, mean observed fork lengths (± 1 SE), mean observed mass, and von Bertalanffy estimates of fork lengths (VB FL) for each sex of cobia from North Carolina and adjacent waters, 1983-94, by estimated age. Results of Richards' (1967 and 1977) studies are presented for comparison. All lengths are in cm.

Sex	Estimated Age	<i>n</i>	FL range	Present Study				Richards (1967) ¹			Richards (1977)	
				\bar{x} observed FL	± 1 SE	\bar{x} mass kg	<i>n</i>	VB ² FL	\bar{x} observed FL	\bar{x} kg	mass VB FL	
Males	1	6	39– 64	50	4	1.3	6	56	54	1.5	31	
	2	22	63– 93	74	2	3.9	13	71	71	3.8	53	
	3	41	68–102	82	1	6.7	23	82	84	7.6	69	
	4	32	82– 97	88	1	8.3	14	89	94	9.6	82	
	5	20	78– 99	92	1	9.4	12	94	101	11.9	91	
	6	7	90–103	95	2	10.6	7	97	104	13.7	99	
	7	6	94–108	100	2	11.5	5	100	105	14.5	104	
	8	8	89–107	99	2	13.6	5	101			108	
	9	6	99–136	107	6	18.3	4	103	109	17.7		
	10	5	101–109	105	1	12.2	1	103	119	19.0		
	11	3	102–109	105	2			104				
	12	0						104				
	13	1		113		19.3	1	104				
	14	1		106		20.0	1	105				
Females	1	3	49– 63	55	4	1.0	1	61	58	1.8	36	
	2	18	57–106	81	3	6.1	16	77	78	4.6	61	
	3	50	79– 99	89	1	8.4	36	89	95	11.1	82	
	4	23	88–132	102	2	12.5	12	99	104	13.2	99	
	5	13	98–113	106	1	14.9	10	107	116	19.7	112	
	6	20	99–126	111	2	17.8	14	113	120	21.8	122	
	7	11	110–126	117	2	21.0	10	117	126	25.1	131	
	8	8	114–128	123	2	23.9	6	121	130	28.4	137	
	9	7	114–134	125	2	24.6	5	124				
	10	3	117–133	127	5	29.7	2	126	133	30.5		
	11	1		121		18.1	1	128				
	12	3	125–130	127	2	28.6	1	130				
	13	2	134–142	138	4	32.0	2	131				

¹ Values converted to metric units from published English units.

² Values are von Bertalanffy estimates of FL based on individual FLs at estimated age.

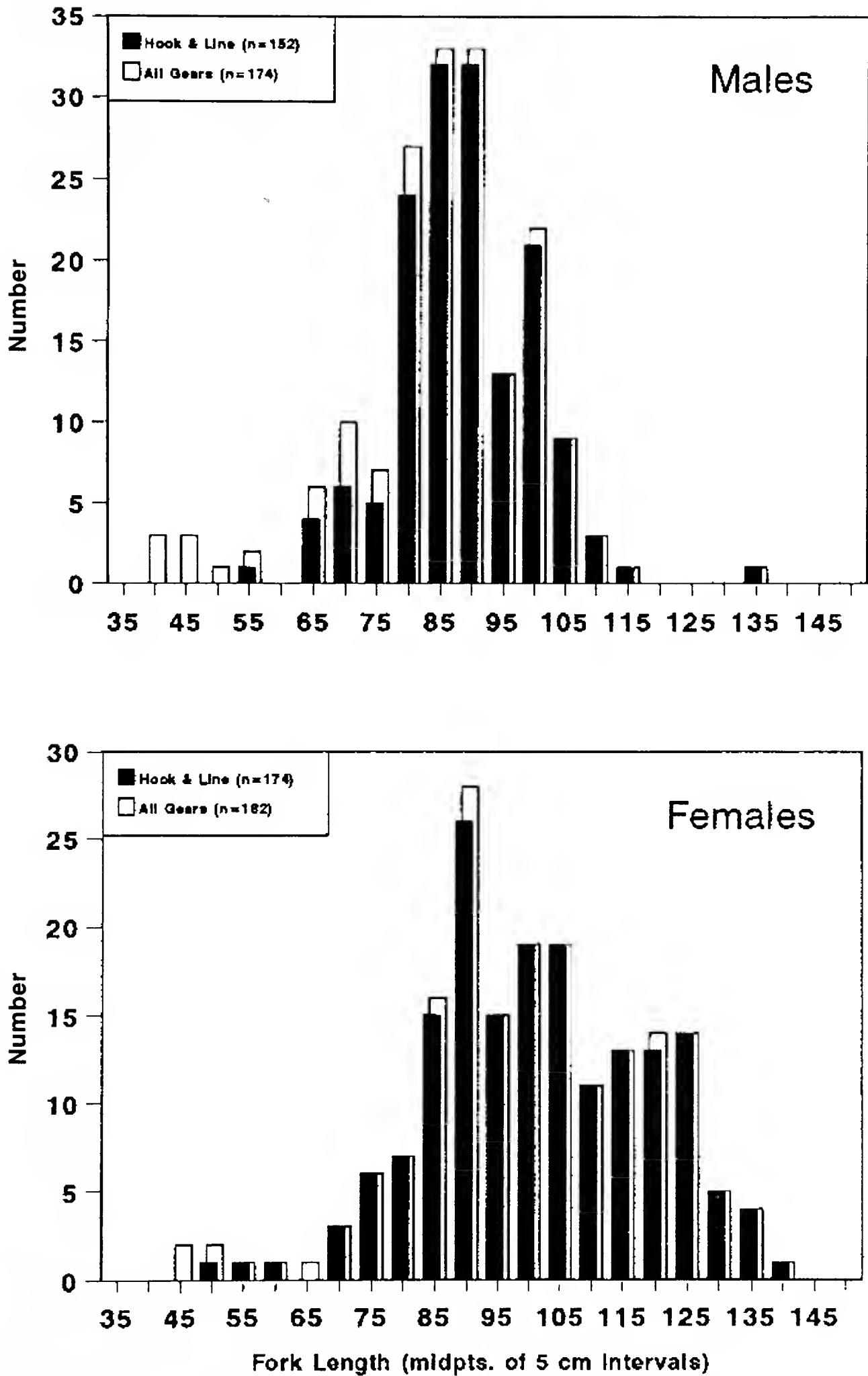


Fig. 3. Fork length frequency distributions (all gears and hook-and-line) by 5-cm increments for male and female cobia from North Carolina and adjacent waters, 1983–94.

Table 3. Von Bertalanffy parameter estimates by sex describing the growth of cobia from North Carolina and adjacent waters, 1983-94; CL = 95% confidence limits. Richards' (1977) estimates shown for comparison.

Sex	Parameter	Estimate	Asymptotic SE	Asymptotic lower	CL upper	Richards' (1977) estimates
Males	l_{∞}	105	1.85	101	108	121
	k	0.37	0.04	0.29	0.45	0.28
	t_0	-1.08	0.29	-1.65	-0.51	-0.06
Females	l_{∞}	135	3.82	127	142	164
	k	0.24	0.03	0.18	0.31	0.23
	t_0	-1.53	0.39	-2.30	-0.77	-0.08

coral patches of low relief (Huntsman 1976). By early May, cobia were found on nearshore artificial reefs and under navigation buoys in the vicinity of Beaufort, Ocracoke, and Hatteras inlets (Manooch et al. 1981). The earliest record for cobia caught by hook-and-line in North Carolina estuarine waters during the study was 8 May 1990. Initial spring catches in the sounds coincided with inshore water temperatures reaching 20 C and higher. Most “inshore” angling activity for cobia was concentrated in Bogue and Back sounds adjacent to Beaufort and Bardens inlets near Cape Lookout, and Pamlico Sound adjacent to Ocracoke and Hatteras inlets near Cape Hatteras (Fig. 1). Traditional fishing locations for cobia in North Carolina’s inlets, sounds, and coastal rivers were poly- to mesohaline waters >5–6 m deep. These sites were characterized by long, straight troughs or embayments (up to several kilometers long and/or wide), often with adjacent feeder creeks or channels, e.g., Bogue Sound, Newport River, and Wallace and Blair channels of Ocracoke Inlet.

Peak catches of cobia in the North Carolina sounds occurred during June, and declined thereafter (Table 4). The latest record for an adult cobia taken by hook-and-line in the Carolina sounds during this study was 18 August 1988. Cobia were captured during summer in the nearshore ocean adjacent to buoys and fishing piers, and over artificial reefs and live bottom areas. Catches were often incidental to bottom fishing or live-bait fishing for other species. During May 1988 and June 1991, catches were poor in the sounds following the passage of unseasonable cold fronts that quickly chilled estuarine water temperatures from 26 C to 19 C and 28 C to 22 C, respectively.

Juvenile cobia also occurred in North Carolina sounds during summer. Young-of-the-year (based on length frequency distributions

Table 4. Number of cobia processed that were and caught by hook-and-line in North Carolina by month and date, 1983-90 (date intervals arbitrarily chosen).

Dates	May	June	July	August	September
1-7	1	45	8	0	0
8-15	5	100	5	0	1
16-22	27	6	3	1	0
23-31	20	33	5	0	0
Totals	53	184	21	1	1

and otolith analyses) were collected in pound nets and long haul nets from Pamlico Sound in August and September (Fig. 3). Age 1 fish occurred in the sounds from late May through mid-September, and most specimens were taken by hook-and-line.

FOOD HABITS

During 1989-1990, 140 cobia stomachs were examined, of which 72.1% ($n = 101$) contained representative food items. *Iri*'s were computed from these samples and nine additional stomachs with food items from 1987 to 1988. Twenty-four species groups of crustaceans, 16 species groups of fishes, and one cephalopod were identified from 110 stomachs (Table 5).

After pooling data from all three sampling areas, the blue crab, *Callinectes sapidus*, had the highest *iri*, followed by the blackcheek tonguefish, *Symphurus plagiatus*, and unidentified fish remains. Other identifiable fishes in the diet with high *iri*'s were pipefishes, *Syngnathus* sp., and the smooth dogfish, *Mustelus canis*. Items apparently incidentally ingested included eelgrass (*Zostera marina*) blades, small fragments of oyster shell (*Crassostrea virginica*), and small gastropods.

In the Beaufort area, the blue crab (Table 6) had the highest *iri*, followed by the smooth dogfish, pipefishes, and dasyatid sting rays. Abundant crustaceans included the iridescent swimming crab, *Portunus gibbesii*, the brown shrimp, *Penaeus aztecus*, and the mantis shrimp, *Squilla empusa*. High-ranking food items from the Hatteras-Ocracoke area (Table 6) were the blackcheek tonguefish and the blue crab. Important food items from offshore waters (Table 6) included the coarsehand lady crab, *Ovalipes stephensoni*, unidentifiable fishes, the blotched swimming crab, *Portunus spinimanus*, and rock shrimps, *Sicyonia* sp.

Among individual prey taxa, elasmobranchs were the largest prey

Table 5. Percent frequency of occurrence (*f*), percent number (*n*), percent mass (*w*), and index of relative importance (*iri*) of food items in cobia stomachs from North Carolina and adjacent waters, 1987-90.

Prey Taxa	<i>f</i>	<i>n</i>	<i>w</i>	<i>iri</i>
Mollusca				
Cephalopoda				
<i>Loligo plei</i>	0.9	0.2	<0.1	<1
Arthropoda				
Crustacea				
Stomatopoda				
<i>Squilla</i> sp.	2.7	0.7	0.4	3
<i>S. empusa</i>	3.6	1.3	2.5	14
<i>S. neglecta</i>	1.8	4.2	2.5	12
Decapoda				
Penaeidae				
<i>Penaeus</i> sp.	3.6	0.9	0.2	4
<i>P. aztecus</i>	6.4	2.9	3.7	42
<i>P. setiferus</i>	0.9	0.2	0.2	<1
<i>Trachypenaeus constrictus</i>	0.9	1.5	<0.1	<1
Sicyoniidae				
<i>Sicyonia</i> sp.	3.6	7.9	2.7	38
Palaemonidae				
<i>Palaemonetes vulgaris</i>	0.9	0.4	<0.1	<1
Crangonidae				
<i>Crangon septemspinosa</i>	4.5	2.6	0.2	13
Upogebiidae				
<i>Upogebia</i> sp.	0.9	0.2	<0.1	<1
Albuneidae				
<i>Albunea gibbesii</i>	0.9	0.2	0.1	<1
Portunidae				
<i>Ovalipes</i> sp.	6.4	3.7	2.0	36
<i>O. ocellatus</i>	2.7	0.9	1.1	5
<i>O. stephensoni</i>	6.4	4.6	4.0	55
<i>Callinectes</i> sp.	7.3	3.3	1.8	37
<i>C. sapidus</i>	30.0	15.4	19.2	1,038
<i>C. similis</i>	3.6	0.9	0.8	6
<i>Portunus</i> sp.	3.6	1.1	0.5	6
<i>P. gibbesii</i>	5.5	2.2	1.8	22
<i>P. spinimanus</i>	2.7	0.7	1.4	6
Unidentified portunid remains	4.5	2.2	0.3	11
Xanthidae				
<i>Menippe mercenaria</i>	0.9	0.4	0.1	<1
Unidentified decapod remains	0.9	0.2	<0.1	<1
Chondrichthyes				
Carcharhinidae				
<i>Mustelus canis</i>	6.4	6.1	21.2	175

Table 5. Continued.

Prey Taxa	<i>f</i>	<i>n</i>	<i>w</i>	<i>iri</i>
Dasyatidae				
<i>Dasyatis</i> sp.	3.6	0.9	12.7	49
Osteichthyes				
Clupeidae				
<i>Opisthonema oglinum</i>	0.9	0.4	0.4	1
Engraulidae				
<i>Anchoa</i> sp.	0.9	1.3	0.1	1
Synodontidae				
<i>Synodus foetens</i>	0.9	0.2	0.3	<1
Batrachoididae				
<i>Opsanus</i> sp.	3.6	1.1	2.7	14
Syngnathidae				
<i>Hippocampus</i> sp.	0.9	0.2	<0.1	<1
<i>Syngnathus</i> sp.	19.1	7.0	2.2	176
Sparidae				
<i>Lagodon rhomboides</i>	0.9	0.2	0.2	<1
Uranoscopidae				
unidentified remains	0.9	0.2	<0.1	<1
Soleidae				
<i>Trinectes maculatus</i>	0.9	0.7	0.4	1
Cynoglossidae				
<i>Symphurus plagiusa</i>	17.3	13.2	6.8	346
Balistidae				
unidentified remains	2.7	1.3	0.1	4
Tetradontidae				
<i>Sphoeroides maculatus</i>	0.9	0.7	1.9	2
Diodontidae				
<i>Chilomycterus schoepfi</i>	0.9	0.2	1.2	1
unidentified fish remains	21.8	7.5	4.5	262

ingested. Smooth dogfish pups ($n = 28$) averaged 42 g; dasyatid sting rays ($n = 4$) averaged 173 g. The largest teleosts consumed were the striped burrfish, *Chilomycterus schoepfi* ($n = 1$, 65 g), the northern puffer, *Sphoeroides maculatus* ($n = 3$, $\bar{x} = 34$ g), and toadfishes, *Opsanus* sp. ($n = 5$, $\bar{x} = 29$ g). Most portunid crabs were less than 7 cm in carapace width (CW) and were ingested whole; commercial-sized blue crabs (ca. 12.5-cm CW) were rarely consumed. Ovalipid crabs were often macerated. Small balistid fishes occurred in the stomachs of juvenile cobia from offshore trawl catches and were among the smallest teleosts consumed ($n = 6$, $\bar{x} = 1$ g).

As cobia increased in size, penaeid shrimps and teleost fishes became relatively less important in the diet, while decapod crabs increased

Table 6. The ten highest ranked prey items in cobia stomachs by sampling area in North Carolina¹, 1987–90.

Beaufort Inlet (n = 40)			Ocracoke-Hatteras Inlets (n = 56)			Offshore Areas (n = 14)		
Prey	iri		Prey	iri		Prey	iri	
<i>Callinectes sapidus</i>	1,609		<i>Symphurus plagiusa</i>	1,311		<i>Ovalipes stephensoni</i>		870
<i>Mustelus canis</i>	802		<i>Callinectes sapidus</i>	1,111		Unidentified fish		654
<i>Syngnathus</i> sp.	236		Unidentified fish	355		<i>Portunus spinimanus</i>		561
<i>Dasyatis</i> sp.	208		<i>Ovalipes</i> sp.	164		<i>Sicyonia</i> sp.		516
Unidentified fish	133		<i>Syngnathus</i> sp.	130		Unident. <i>Balistidae</i>		277
<i>Portunus gibbesii</i>	89		<i>Sicyonia</i> sp.	69		<i>Syngnathus</i> sp.		182
<i>Penaeus aztecus</i>	73		<i>Opsanus</i> sp.	56		<i>Trachypenaeus constrictus</i>		95
<i>Squilla empusa</i>	69		<i>Penaeus aztecus</i>	42		<i>Anchoa</i> sp.		90
<i>Callinectes</i> sp.	55		<i>Crangon septemspinosa</i>	32		<i>Synodus foetens</i>		41
<i>Symphurus plagiusa</i>	38		<i>Callinectes</i> sp.	31		<i>Symphurus plagiusa</i>		35

¹ n = number of stomachs examined by locality.

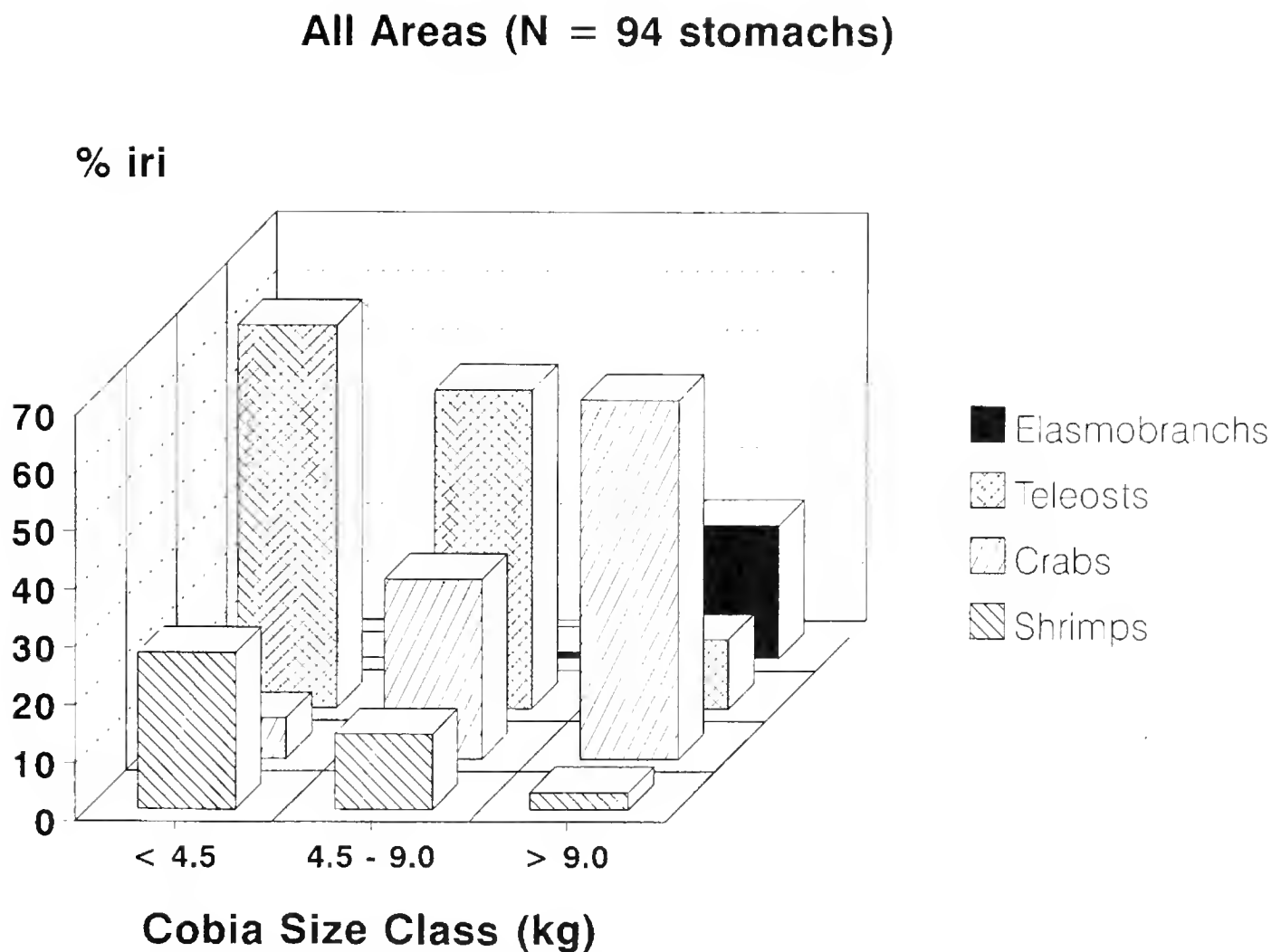


Fig. 4. Percent *iri*'s for various prey groups by cobia mass interval (intervals arbitrarily chosen).

in importance (Fig. 4). Elasmobranchs, that is, the smooth dogfish and dasyatid sting rays, were consumed almost exclusively by cobia greater than 9 kg. Seventy-five percent (50 of 67) of female cobia from North Carolina sounds and inlet areas had food in their stomach at capture, suggesting that these areas may be foraging grounds before and after spawning.

REPRODUCTION

One hundred and twenty-seven male and 113 female cobia were sexed and staged for maturity in the field. Most male cobia were developing or ripe (Table 7). The latter state was characterized by active spermatogenesis and copious amounts of sperm within testicular ducts (Fig. 5a). Mean *gsi*'s for males increased from 3.0 (SD = 1.2, $n = 14$) in May, to 4.7 (SD = 1.5, $n = 44$) in June, then declined slightly to 4.4 (SD = 1.6, $n = 7$) in July. Most male cobia were sexually mature by 60–65 cm FL (Table 7), or age 2.

Most female cobia examined were staged as developing (Table 7), and most were sexually mature by 80 cm FL, or age 2. Histological sections revealed that the ovaries of early developing females had

Table 7. Cobia from North Carolina and adjacent waters, 1983–94, in various stages of sexual development by 5-cm-FL intervals.

Midpoint 5-cm-FL	Males		Females		
	Immature	Developing and Ripe	Immature	Developing	Ripe
≤ 50	5	0	4	0	0
55	1	0	1	0	0
60	1	3	1	0	0
65	0	6	1	0	0
70	0	5	1	2	0
75	0	22	5	0	0
80	0	23	0	6	0
85	0	25	0	11	0
90	0	11	0	19	1
95	0	17	0	8	0
100	0	7	0	9	0
105	0	0	0	11	0
110	0	1	0	9	0
115	0	0	0	5	0
120			0	6	0
125			0	8	0
130			0	2	0
135			0	2	0
140			0	1	0
Totals	7	120	13	99	1

many small basophilic oocytes with a few early vitellogenic oocytes (Fig. 5b), whereas the ovaries of late developing females had large (ca. 750 μ m), yolk-filled oocytes (Fig. 5c). Only one female had hydrated oocytes; it was uncertain if this fish was caught in estuarine or oceanic waters. A few females (collected in early June 1990) showed follicular atresia indicative of a recent spawn, yet also possessed numerous large oocytes, suggestive of an incipient spawn (Fig. 5d).

Mean *gsi*'s for female cobia were high in May at 5.5 (SD = 2.2, *n* = 8), peaked in June at 5.7 (SD = 2.1, *n* = 49), and declined slightly in July at 5.3 (SD = 2.2, *n* = 8). The largest ovaries excised weighed 2.49 kg (7 June) and were in a female weighing 25.4 kg. Peak spawning in June 1989 was confirmed by neuston net collections of cobia eggs from a channel in the lower Newport River estuary about 3 km from Beaufort Inlet (Fig. 1) (L. Settle, National Marine Fisheries Service, Beaufort, North Carolina, unpublished data). During 10 sampling dates between 14 June and 18 August, peak cobia egg

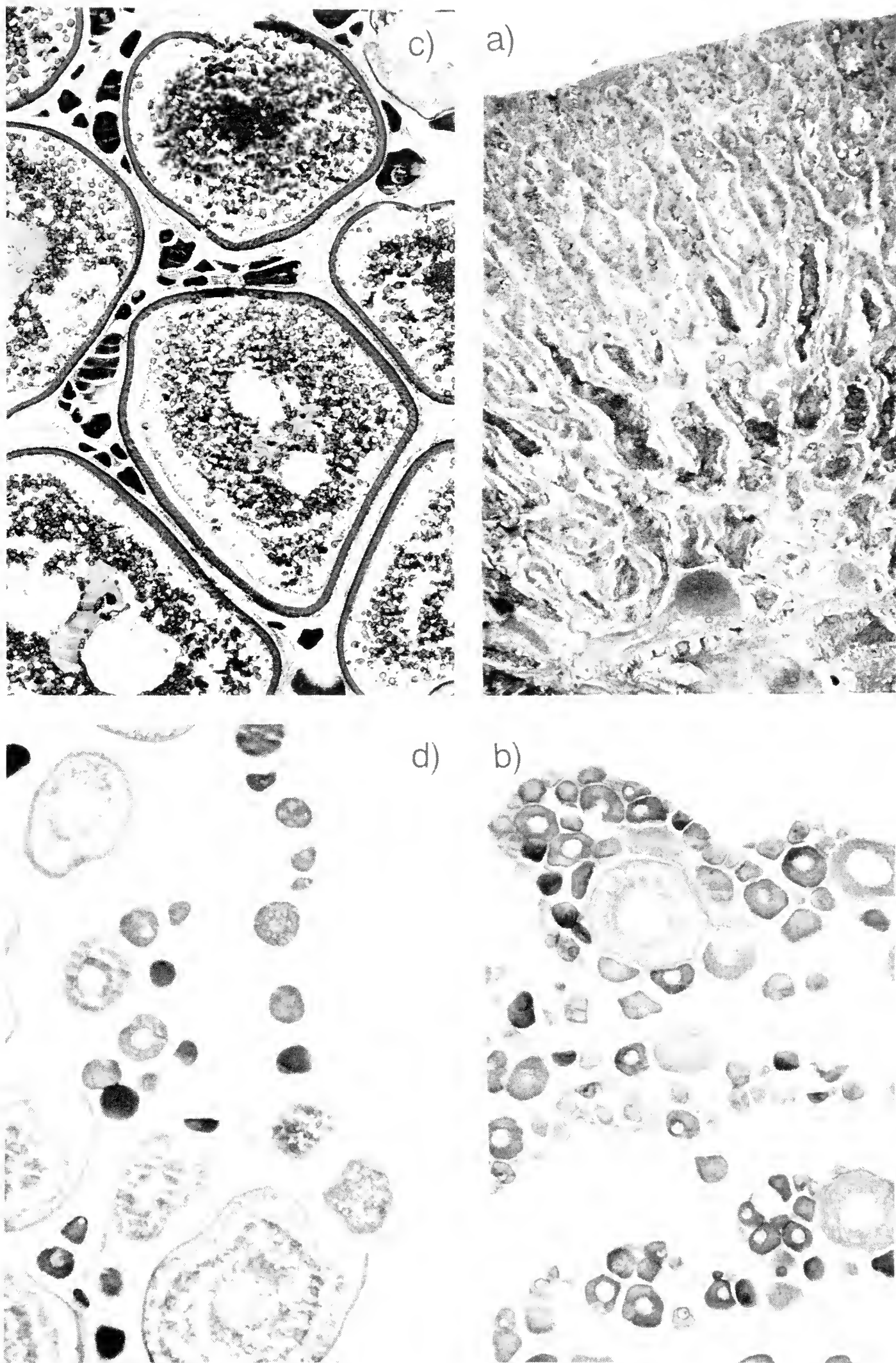


Fig. 5. Histologic preparations of cobia gonad sections: a) ripe male (70 cm FL), b) early developing female (80 cm FL), c) late developing female (104 cm FL), d) partially spent female (88 cm FL), but with numerous large oocytes.

concentrations occurred on 23 June (67 eggs/100 m³), with minor peaks occurring on 11 July (44 eggs/100 m³), and 4 August (28 eggs/100 m³). Moreover, results of a concurrent ichthyoplankton survey (1989) near Ocracoke Inlet indicated that cobia eggs were one of the most common taxa encountered during May and June (W. Hettler, National Marine Fisheries Service, Beaufort, North Carolina, personal communications).

DISCUSSION

Cobia occurred in the sounds and ocean inlets of North Carolina from May to July, and as Richards (1967) observed in Chesapeake Bay, initial spring catches by sport fishermen were coincident with nearshore and estuarine water temperatures rising above 20 C. Cold fronts during May and June accompanied by strong northeast winds chilled inshore water temperatures and adversely affected spring catches of cobia in North Carolina. During August and into fall, cobia were found primarily in coastal oceanic waters. Cobia reside in other major estuaries along the United States Atlantic coast during spring and summer, e.g., Port Royal and St. Helena sounds in South Carolina (Moore et al. 1980) and Chesapeake Bay (Richards 1967). This contrasts with the northern Gulf of Mexico where most cobia occur along shallow coastal waters of the Gulf and offshore in association with oil and gas platforms and rafts of *Sargassum* (Ditty and Shaw 1992).

It is unclear where cobia from the south Atlantic coast of the United States overwinter. Winter trawl surveys by South Carolina's Marine Resources Monitoring, Assessment and Prediction Program (South Carolina Marine Resources Research Institute, Charleston, South Carolina, unpublished data) captured cobia ($n = 22$, range = 40-127 cm, $\bar{x} = 84$ cm) during January and February between Cape Fear, North Carolina, and Cape Canaveral, Florida, in 31-75 m depths where water temperatures ranged from 15.9 to 20.8 C (also see Wenner et al. 1979). Cobia taken by various commercial gears (hand, troll, and long lines) have been processed by port agents in North Carolina during all quarters of the year, 1983-91 (L. Mercer, North Carolina Division of Marine Fisheries, Morehead City, North Carolina, personal communications). These findings suggested that off the south Atlantic coast of the United States cobia may overwinter on the outer half of the continental shelf.

Although Richards (1967) used scales to age cobia from Chesapeake Bay, I found that acetate impressions of cobia scales were difficult to interpret for annuli. Alternating translucent and opaque zones of cross-sectioned sagittae were distinct, although I was unable to validate their annual nature. Nevertheless, indirect evidence supported the validity

of opaque zones as annuli. First, mean size of cobia increased with opaque zone count. Second, young-of-the-year cobia (based on length frequency distributions) had no opaque zone distal to the sagittal core or focus, whereas age 1 fish had one opaque zone distal to the sagittal core. Moreover, recent research in the northern Gulf of Mexico (Franks et al. 1991, Thompson et al. 1991) confirmed the validity of the formation of one translucent and one opaque zone on cobia sagittae each year.

Assuming that opaque zones on cobia sagittae were valid annuli, my results indicated that cobia grew rapidly during the first few years of life, and by age 3 mean mass ranged from 6 to 8 kg. Results from public tagging programs report equally dramatic growth for recaptured specimens (Anonymous 1986, Richard 1989, Franks 1995). My study agreed closely with Richards (1967) on mean length for both sexes at age 1 and 2 (Table 2). For age 3 and older, Richards (1967) reported that mean sizes were larger. Eleven specimens were estimated as age 11 to 14, while Richards' (1967) maximum age for cobia was age 10. Perhaps, erosion on scale edges caused him to underestimate cobia ages, as has been shown in other fishes (Chilton and Stocker 1987).

Male cobia have a higher growth coefficient, k , than females, and the difference between sexes was greater for my study (0.37 to 0.24) than previous work (0.28 to 0.23; Richards 1977). Mean asymptotic FLs (Table 3) for both sexes were lower than Richards (1977) reported, possibly reflecting a greater availability of larger cobia in Chesapeake Bay during the 1960s. Age 3 females ($n = 50$) predominated in the present study, whereas Richards (1967) found age 5 females ($n = 34$) were most numerous. No doubt, estimates of mean asymptotic size in the present study were underestimates as the current North Carolina state record cobia (1988) weighed 46.7 kg.

Cobia were primarily demersal feeders along the North Carolina coast, and they preyed on portunid crabs, penaeid shrimps, stomatopods, numerous teleosts, and small elasmobranchs. Overall, the blue crab was the most important food item in the cobia diet, which reinforces the colloquial name of "crab-eater" used along the southeastern coast of the United States (Knapp 1951, Manooch 1984). Most portunids were ingested whole, except for *Ovalipes* which was usually macerated. Similar to the results of the present study, Knapp (1951) found demersal prey, such as portunids, stomatopods, penaeids, and eels in cobia stomachs from the northern Gulf of Mexico. Cobia from the western Indian Ocean consumed mostly portunids, cephalopods, and eels (Darracott 1977). In the sounds of North Carolina, cobia greater than 9 kg showed a predilection for smooth dogfish pups and small dasyatid sting rays, and these were among the largest prey items ingested. Cobia may

be one of the few teleosts that regularly consumed small elasmobranchs.

Field inspections and histological sections of cobia gonads indicated that most adult cobia were developing and/or ripe as they entered North Carolina waters in spring. Males became sexually mature by 60–65 cm (age 2), and females by 80 cm (age 2). Richards (1967) stated that the smallest mature male in his collections measured 51.8 cm (“second....year of life”) and that the smallest mature female measured 69.6 cm (“third year of life”), but he did not include maturity schedules.

Cobia spawned in North Carolina coastal waters from May through July, with peak spawning in June. In Virginia waters, cobia spawned mid-June through mid-August, as determined by ichthyoplankton surveys (Joseph et al. 1964). In the northern Gulf of Mexico, cobia arrived in coastal waters during April and May in prespawning condition and exhibiting peak *gsi* values (Biesiot et al. 1994). Some female cobia collected during June in North Carolina showed follicular atresia in the ovaries indicative of a recent spawn, yet also had numerous and adjacent, large oocytes, suggesting another potential spawning event. Data on ova diameters presented by Richards (1967) and work by Thompson et al. (1991) and Biesiot et al. (1994) in the northern Gulf of Mexico support the concept of batch spawning in cobia.

Precise location of cobia spawning areas along the North Carolina coast was uncertain, although my results suggested that cobia spawned adjacent the state’s major ocean inlets. Likewise, Joseph et al. (1964) found that cobia spawned off the mouth of Chesapeake Bay in Virginia. Collections of cobia eggs in the Gulf Stream off Cape Hatteras, North Carolina, by Hassler and Rainville (1975) (almost 2,000 eggs in 10 collecting trips, May–June 1974) contrast an inlet spawning area hypothesis.

In summary, cobia inhabited coastal sounds and inlet areas of North Carolina from May through July. Specimens greater than 15 kg were common, hence the species’ popularity with inshore recreational anglers. Cobia consumed a variety of demersal crustaceans and fishes; of the former, the blue crab was the most important. Spawning probably peaked during June in ocean waters adjacent major inlets. Management regulations adopted by North Carolina in 1991 prohibiting possession of cobia less than 84 cm were effective, and few fish below the minimum possession size were encountered between 1991 and 1994. Migratory routes and overwintering grounds of cobia along the south Atlantic coast of the United States are unclear. Comprehensive tagging of cobia along the south Atlantic coast of the United States and in Chesapeake Bay would help clarify (1) coast-wide migration patterns, (2) ingress and egress from estuaries to ocean, (3) fidelity to specific estuaries, and (4) movements into the northern Gulf of Mexico.

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A Review of Stonefly Records (Plecoptera: Hexapoda) of North Carolina and South Carolina

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Abstract—The stoneflies (Plecoptera) of North Carolina and South Carolina are comprehensively reviewed for the first time. One hundred and thirteen and 83 stonefly species are recorded from North Carolina and South Carolina, respectively. Thirteen new state records are given for North Carolina and two for South Carolina. An additional 22 species are listed that may be eventually collected in either state.

Unzicker and McCaskill (1982) presented the first comprehensive checklist of 131 stoneflies known or likely to occur in North Carolina and South Carolina. However, as Lenat and Penrose (1987) pointed out, this list did not distinguish between North Carolina and South Carolina, and validation of individual state records requires examination of the literature. Stark et al. (1986) and Stewart and Stark (1988) have provided recent compilations of stonefly species records for North America, listing 75 and 77 species for North Carolina and 77 and 79 for South Carolina, respectively. However, all three lists contain omissions or list species identified in error (Table 1). For example, Stark et al. (1986) did not list *Taeniopteryx burksi* Ricker and Ross, *T. lonicera* Ricker and Ross, and *T. meteui* Ricker and Ross from North Carolina despite the records published by Ricker and Ross (1968) or by Fullington and Stewart (1980). Notations in Table 1 are included to help clarify taxonomic changes and to distinguish between the lists.

In addition to the notations in Table 1, the following species should be deleted from the list of North Carolina and South Carolina stoneflies: (1) *Paracapnia opis* (Newman)—this species is northeastern in distribution (Stark et al. 1986), previous determinations were in error, and all records are referable to *P. angulata* Hanson; (2) *Leuctra tenella* Provancher—a species very similar to *L. carolinensis*, and *L. maria* Hanson are also considered northeastern in distribution (Stark et al. 1986); (3) the nearest records for *Alloperla imbecilla* (Say) are from northwestern Virginia and West Virginia (Baumann 1974, Surdick 1985); (4) *Isoperla nana* (Walsh)—a small black *Isoperla* is considered a northeastern and central species (Stark et al. 1986); and (5) *Isogenoides doratus* Frison—a species that is restricted to the upper Midwest and Northeast (Stark et al. 1986).

In addition, *Allocapnia granulata* (Claassen), *A. mystica* Frison, and *A. pygmaea* (Burmeister) were listed by Unzicker and McCaskill (1982), but no verifiable records for North Carolina and South Carolina are available.

The following 13 new state records for North Carolina are based on specimens deposited in the C. P. Gillette Museum of Arthropod Diversity, Colorado State University (CSU) or the North Carolina Division of Environmental Management, Water Quality Section (NCDDEM) collections. Nine species are also noted that have been reported since Stewart and Stark (1988) for North Carolina:

Leuctra ferruginea (Walker) (Huryn and Wallace, 1987).

Megaleuctra williamsae Hanson - Macon Co., trib. Cullasaja R., 24 May 1994, CSU; Haywood Co., R. F. Cove Cr., 23 May 1994, CSU; Jackson Co., Mull Cr., 23 May 1993, CSU.

Prostoia hallasi Kondratieff and Kirchner - Gates Co., Great Dismal Swamp, 26 March 1992, CSU.

Amphinemura nigritta (Provancher) - Avery Co., Linville R., 18 May 1994, CSU; Haywood Co., East Fork Pigeon R., 23 May 1990, CSU; Yancey Co., trib. to Cane R., 18 May 1994, CSU.

Zapada chila (Ricker) (Ashe Co., Lenat and Penrose, 1987).

Oemopteryx contorta (Needham and Claassen) - Moore Co., Suck Cr., Feb., 1984, NCDDEM.

Strophopteryx limata (Frison) - Haywood Co., Cataloochee Cr., Great Smoky Mt. Nat. Pk., 23 May 1993, CSU.

Agnetina flavescens (Walsh) - Clay Co., Fires Cr., April 1987, NCDDEM; Ashe Co., South Fork New R., March 1990, NCDDEM.

Acroneuria frisoni Stark and Brown - Jackson Co., Dillsboro, 5 Aug. 1982, CSU.

- A. lycorias* (Newman) - Harnett Co., Barbecue Swamp, Nov., 1988, NCDEM.
- Paragnetina kansensis* Banks (Duplin Co., Robeson Co., Lenat and Penrose 1987).
- Neoperla clymene* (Newman) - Ashe Co., South Fork New River, CSU.
- Diploperla duplicata* (Banks) (Guilford Co., Forsyth Co., Burke Co., Transylvania Co., Lenat and Penrose 1987).
- D. morgani* Kondratieff and Voshell (Surry Co., Lenat and Penrose 1987).
- Helopicus bogaloosa* Stark and Ray (Richmond Co., Robeson Co., Lenat and Penrose 1987).
- Isoperla burksi* Frison (Chatham Co., Davie Co., Duplin Co., Randolph Co., Lenat and Penrose 1987).
- I. dicala* Frison - Ashe Co., South Fork New River, CSU; Jackson Co., CSU.
- I. frisoni* Illies (Cherokee Co., Stokes Co., Lenat and Penrose 1987).
- I. lata* Frison - Clay Co., Fires Cr., 18 April 1988, NCDEM; Big Cr., Haywood Co., Great Smoky Mt. Nat. Pk., CSU.
- I. namata* Frison (Lenat 1983).
- I. slossonae* (Banks) (Ashe Co., Lenat and Penrose 1987); Transylvania Co. NCDEM.
- I. transmarina* (Newman) - Moore Co., Drowning Cr., NCDEM.
- Pteronarcys dorsata* (Say) - Ashe Co., Catawba Co., Scotland Co. NCDEM.

Two new South Carolina state records are based on specimens in the C. P. Gillette Museum of Arthropod Diversity, Colorado State University (CSU) from South Carolina, and there is one additional new literature record:

- Isoperla burksi* - Edgefield Co., Stevens Cr., 24 May 1984, CSU.
- I. davisii* James - Edgefield Co., Stevens Cr., 24 May 1984, CSU.
- Taenionema atlanticum* Ricker and Ross ("South Carolina," Stanger and Baumann 1993).

Several undescribed species of *Isoperla* are known from both states, and S. W. Szczytko (University of Wisconsin, Stevens Point) is presently describing these species.

Table 2 lists the species of stoneflies known from North Carolina (113 species) and South Carolina (83 species). This table also includes 22 species marked with a "*" that occur in surrounding states and could be collected in either state.

Morse et al. (1993) noted that at least 12 stonefly species, *Allocapnia fumosa* Ross, *Megaleuctra williamsae*, *Strophopteryx inaya* Ricker and Ross, *Sweltsa urticae* (Ricker), *Tallaperla elisa* Stark, *Acroneuria arida*

(Hagen), *Beloneuria georgiana* (Banks), *B. stewarti* Stark and Szczytko, *Diploperla morgani*, *Isoperla bellona* Banks, *I. distincta* Nelson, and *Oconoperla innubila* (Needham and Claassen) occur in one or both states and are rare and vulnerable species, sensitive to human induced impacts. As Baumann (1979) clearly indicated, stoneflies are good indicators of ecosystem quality at all scales. All the species listed above by Morse et al. (1993) are considered southern Appalachian in distribution. This geographical region is being directly impacted by regional influences (e.g. acid deposition) and local landscape changes (e.g. agriculture, rural developments, and timber harvest). The very diverse stonefly fauna of both states is indicative of a wide range of high quality lotic aquatic habitats, which need active protection.

Table 1. A comparison of three stonefly (Plecoptera) species lists for North Carolina (NC) and South Carolina (SC).

	Unzicker and McCaskill (1982)	Stark et al. (1986)	Stewart and Stark (1988)
Euholognatha			
Capniidae			
<i>Allocapnia aurora</i> Ricker	X	NC,SC	NC,SC
<i>A. brooksi</i> Ross	X ¹		
<i>A. fumosa</i> Ross	X	NC	NC
<i>A. granulata</i> (Claassen)	X		
<i>A. loshada</i> Ricker	X ¹		
<i>A. mystica</i> Frison	X		
<i>A. nivicola</i> (Fitch)	X	NC	NC
<i>A. pygmaea</i> (Burmeister)	X		
<i>A. recta</i> (Claassen)	X	NC,SC	NC,SC
<i>A. rickeri</i> Frison	X	NC	NC
<i>A. stannardi</i> Ross	X	NC	NC
<i>A. virginiana</i> Frison	X	NC,SC	NC,SC
<i>A. wrayi</i> Ross	X	NC,SC	NC,SC
<i>Nemocapnia carolina</i> Banks	X	NC,SC	NC,SC
<i>Paracapnia angulata</i> Hanson	X	NC	NC
<i>P. opis</i> (Newman)	X		
Leuctridae			
<i>Leuctra alexanderi</i> Hanson	X	NC,SC	NC,SC
<i>L. biloba</i> Claassen	X	NC	NC
<i>L. carolinensis</i> Claassen	X	NC,SC	NC,SC
<i>L. ferruginea</i> (Walker)	X	SC	SC
<i>L. grandis</i> Banks	X	NC	NC
<i>L. maria</i> Hanson	X		

Table 1. Continued.

	Unzicker and McCaskill (1982)	Stark et al. (1986)	Stewart and Stark (1988)
<i>L. mitchellensis</i> Hanson	X	NC	NC
<i>L. moha</i> Ricker	X	SC	SC
<i>L. monticola</i> Hanson	X	NC,SC	NC,SC
<i>L. nephophila</i> Hanson	X	NC	NC
<i>L. sibleyi</i> Claassen	X	NC,SC	NC,SC
<i>L. tenella</i> Provancher	X		
<i>L. tenuis</i> (Pictet)	X	SC	SC
<i>L. triloba</i> Claassen	X	NC,SC	NC,SC
<i>L. variabilis</i> Hanson	X		
<i>Megaleuctra williamsae</i> Hanson	X	SC	SC
<i>Paraleuctra sara</i> (Claassen)	X	NC,SC	NC,SC
Nemouridae			
<i>Amphinemura delosa</i> (Ricker)	X		
<i>A. nigritta</i> (Provancher)	X	SC	SC
<i>A. wui</i> (Claassen)	X	NC,SC	NC,SC
<i>Paranemoura perfecta</i> (Walker)	X	NC	NC
<i>Prostoia completa</i> (Walker)	X	NC,SC	NC,SC
<i>P. similis</i> (Hagen)	X	SC	SC
<i>Shipsa rotunda</i> (Claassen)	X	SC	NC ² ,SC
<i>Soyedina carolinensis</i> (Claassen)	X	NC	NC
<i>Zapada chila</i> (Ricker)	X ¹		
Taeniopterygidae			
<i>Boltoperla rossi</i> (Frison)	X	NC	NC
<i>Oemopteryx contorta</i> (Needham and Claassen)	X		
<i>Strophopteryx</i>			
<i>appalachia</i> Ricker and Ross	X ¹	NC	NC
<i>S. fasciata</i> (Burmeister)	X	NC,SC	NC,SC
<i>S. inaya</i> Ricker and Ross	X	NC,SC	NC,SC
<i>S. limata</i> (Frison)	X ¹		
<i>Taenionema</i>			
<i>atlanticum</i> Ricker and Ross	X	NC	NC
<i>Taeniopteryx burksi</i> Ricker and Ross	X	(3)	NC ³
<i>T. lita</i> Frison	X	NC,SC	NC,SC
<i>T. lonicera</i> Ricker and Ross	X	(3) SC	(3) SC
<i>T. maura</i> (Pictet)	X	NC,SC	NC,SC
<i>T. metequi</i> Ricker and Ross	X		

Table 1. Continued.

	Unzicker and McCaskill (1982)	Stark et al. (1986)	Stewart and Stark (1988)
<i>T. parvula</i> Banks	X	(3) SC	(3) SC
<i>T. robinae</i> Kondratieff and Kirchner		SC	SC
<i>T. ugola</i> Ricker and Ross	X ¹		
Systellognatha			
Chloroperlidae			
<i>Alloperla atlantica</i> Baumann	X	NC,SC	NC,SC
<i>A. caudata</i> Frison	X	(4)	
<i>A. chloris</i> Frison	(5)		
<i>A. imbecilla</i> (Say)	X ¹		
<i>A. nanina</i> (Banks)	X ⁶	NC,SC	NC,SC
<i>A. neglecta</i> Frison	X	NC	NC
<i>A. usa</i> Ricker	X ¹	(7) SC	SC
<i>Haploperla brevis</i> (Banks)	X ⁸	NC,SC	NC,SC
<i>Rasvena terna</i> (Frison)	X ¹	(9)	
<i>Suwallia marginata</i> (Banks)	(10)		
<i>Sweltsa lateralis</i> (Banks)	X	NC,SC	NC,SC
<i>S. mediana</i> (Banks 1911)	X	NC	NC
<i>S. onkos</i> (Ricker)		NC ¹¹	NC ¹¹
<i>S. urticae</i> (Ricker 1952)	X	NC	NC
<i>Utaperla</i> sp.	X ¹²		
Peltoperlidae			
<i>Peltoperla ada</i> Needham and Smith	X ^{1,13}		
<i>Peltoperla arcuata</i> Needham	X ¹		
<i>Tallaperla anna</i> (Needham and Smith)	X ^{1,14}	NC,SC	NC,SC
<i>T. cornelia</i> (Needham and Smith)		NC,SC	NC,SC
<i>T. elisa</i> Stark		NC,SC	NC,SC
<i>T. laurie</i> (Ricker)	X ¹⁴	NC,SC	NC,SC
<i>T. maria</i> (Needham and Smith)	X ¹⁴	NC,SC	NC,SC
<i>Viehoperla zipha</i> (Frison)	X ¹³		
<i>Viehoperla ada</i> (Needham and Smith)		NC,SC	NC,SC
Perlidae			
<i>Acroneuria abnormis</i> (Newman)	X	NC,SC	NC,SC
<i>A. arenosa</i> (Pictet)	X	SC	SC
<i>A. arida</i> (Hagen)	X	NC	NC
<i>A. carolinensis</i> (Banks)	X	NC,SC	NC,SC

Table 1. Continued.

	Unzicker and McCaskill (1982)	Stark et al. (1986)	Stewart and Stark (1988)
<i>A. evoluta</i> Klapalek	X ^{1,15}		
<i>A. filicis</i> Frison	X	SC	SC
<i>A. internata</i> (Walker)	X ¹		
<i>A. lycorias</i> (Newman)	X ¹		
<i>A. mela</i> Frison	X ¹⁵		
<i>A. perplexa</i> Frison	X ¹		
<i>A. petersi</i> Stark and Gaufin	X ¹		
<i>Aagnetina annulipes</i> (Hagen)			SC
<i>A. capitata</i> (Pictet)		NC,SC ¹⁶	
<i>A. flavescens</i> (Walsh)			SC
<i>Attaneuria ruralis</i> (Hagen 1861)	X	NC,SC	NC,SC
<i>Beloneuria georgiana</i> (Banks)	X	NC	NC
<i>B. stewarti</i> Stark and Szczytko	X	NC,SC	NC,SC
<i>Eccoptura xanthenes</i> (Newman)	X	NC,SC	NC,SC
<i>Hansonoperla appalachia</i> Nelson	X ¹		SC
<i>Neoperla carlsoni</i> Stark and Baumann	X	SC	SC
<i>N. clymene</i> (Newman)	X		
<i>N. freytagi</i> Stark and Baumann	X	SC	
<i>N. occipitalis</i> (Pictet) ¹⁷			SC
<i>Paragnetina fumosa</i> (Banks)	X	NC,SC	NC,SC
<i>P. ichusa</i> Stark and Szczytko		NC,SC	NC,SC
<i>P. immarginata</i> (Say)	X	NC,SC	NC,SC
<i>P. kansensis</i> (Banks)	X	SC	SC
<i>P. media</i> (Walker)	X		
<i>Perlesta frisoni</i> Banks	X	NC,SC	NC,SC
<i>P. placida</i> (Hagen)	X	SC	
<i>P. placida</i> (Hagen) complex ¹⁸			NC,SC
<i>Perlinella drymo</i> (Newman)	X	SC	NC,SC
<i>P. ephyre</i> (Newman)	X	SC	SC
<i>P. fumipennis</i> (Walsh) ¹⁹	X		SC
<i>P. zwicki</i> Kondratieff, Kirchner and Stewart			SC
<i>Phasganophora capitata</i> (Pictet)	X ²⁰		
Perlodidae			
<i>Clioperla clio</i> (Newman)	(²¹)	NC,SC	NC,SC
<i>Cultus decisus</i> (Walker)	X ²²	NC	NC
<i>Diploperla duplicata</i> (Banks)	X	SC	SC

Table 1. Continued.

	Unzicker and McCaskill (1982)	Stark et al. (1986)	Stewart and Stark (1988)
<i>Helopicus bogaloosa</i> Stark and Ray		SC	SC
<i>H. subvarians</i> (Banks)	X	NC,SC	NC,SC
<i>Hydroperla fugitans</i> (Needham and Claassen)	X ²³		
<i>Isogenoides doratus</i> (Frison)	X ¹		
<i>I. hansonii</i> (Ricker)	X	NC	NC
<i>I. varians</i> (Walsh)	X	SC	SC
<i>Isoperla bellona</i> Banks	X	NC	NC
<i>I. bilineata</i> (Say)	X	NC	NC
<i>I. clio</i> (Newman)	X ²¹		
<i>I. cotta</i> Ricker	X	SC	SC
<i>I. dicala</i> Frison	X	SC	SC
<i>I. distincta</i> Nelson	X ¹	NC,SC	NC,SC
<i>I. holochlora</i> (Klapalek)	X	NC,SC	NC,SC
<i>I. lata</i> Frison	X ¹		
<i>I. marlynia</i> Needham and Claassen	X	SC	SC
<i>I. nana</i> (Walsh)	X		
<i>I. orata</i> Frison	X	NC,SC	NC,SC
<i>I. similis</i> (Hagen)	X	NC,SC	NC,SC
<i>Malirekus hastatus</i> (Banks)	X	NC,SC	NC,SC
<i>Oconoperla innubila</i> (Needham and Claassen) ²⁴		NC,SC	NC,SC
<i>Remenus bilobatus</i> (Needham and Claassen)	X	NC,SC	NC,SC
<i>Yugus arinus</i> (Frison)	X	NC,SC	NC,SC
<i>Y. bulbosus</i> (Frison)	X	NC,SC	NC,SC
<i>Y. innubilis</i> (Needham and Claassen)	X ²⁴		
Pteronarcyidae			
<i>Pteronarcys biloba</i> (Newman)	X ²⁵	NC,SC	NC,SC
<i>P. dorsata</i> (Say)	X	SC	SC
<i>P. proteus</i> (Newman)	X	NC,SC	NC,SC
<i>P. scotti</i> (Ricker)	X	NC,SC	NC,SC

¹ Listed by Unzicker and McCaskill (1982) “as likely to occur in North or South Carolina, but presence has not yet been confirmed.”

² Listed only by Stewart and Stark (1988) in the “Species of Nymphs Examined” and a specimen is illustrated from Davie County, North Carolina, Yadkin River.

Table 1. Continued (Footnotes).

- ³ Ricker and Ross (1968) listed records for these species. Additionally, Stewart and Stark (1988) listed *Taeniopteryx burksi* in the "Species of nymphs examined," but not in the "North American Species List and Distribution."
- ⁴ Surdick (1985) listed Buncombe County and Great Smoky Mountain National Park, North Carolina.
- ⁵ Surdick (1985) listed Buncombe County, North Carolina.
- ⁶ Listed by Unzicker and McCaskill (1982) as *Sweltsa nanina*.
- ⁷ Surdick (1985) listed Buncombe County, McDowell County, and Yancey County, North Carolina.
- ⁸ Listed by Unzicker and McCaskill (1982) as *Hastaperla brevis*, Zwick (1977) discusses the generic synonymy.
- ⁹ Surdick (1985) listed this species from Great Smoky Mountain National Park, North Carolina.
- ¹⁰ Surdick (1985) listed Yancey County and Great Smoky Mountain Park, North Carolina.
- ¹¹ Surdick (1985) did not list *Sweltsa onkos* from North Carolina, presumably older records are misidentifications of *S. mediana*.
- ¹² This generic record is based on nymphs, presumably misidentifications of nymphs of *Alloperla usa*? *Utaperla gaspesiana* Harper and Roy is known from West Virginia.
- ¹³ This species is now included in the genus *Viehoperla*, and *V. zipha* is considered a synonym of *V. ada* (Stark and Stewart 1981).
- ¹⁴ This species is now included in the genus *Tallaperla* (Stark and Stewart 1981).
- ¹⁵ Stark and Brown (1991) studied the holotype of *Acroncuria evoluta* and considered *A. mela* a synonym.
- ¹⁶ The records for this species in Stark et al. (1986) are composite, including both *Aguetina annulipes* and *A. flavescens*, which were distinguished by Stark (1986). The latter reference did not list any records for *A. capitata* from North Carolina.
- ¹⁷ Stark (1990) synonymized *Neoperla freytagi* with *N. occipitalis* (Pictet)
- ¹⁸ Stark (1989) divided the *Perlesta placida* complex into 12 species. Stark (1989) provided records for three species, *P. placida*, North Carolina; *P. frisoni*, Haywood County, North Carolina; Oconee County, Pickens County, South Carolina; *P. nelsoni*, Haywood County, Swain County, North Carolina; Oconee County, South Carolina.
- ¹⁹ Kondratieff et al. (1988) synonymized *Perlinella fumipennis* with *P. ephyre* and described *P. zwicki* for the species formerly identified as *P. fumipennis* from the Southeast.
- ²⁰ Zwick (1984) established the synonymy between *Aguetina* and *Phasganophora*. See note 16.
- ²¹ Szczytko and Stewart (1981) included *Isoperla clio* in *Clioperla*.
- ²² Stark et al. (1988) reviewed this species complex and recognized two species, *Cultus decusus* with two subspecies and *C. verticalis* (Banks). *C. d. isolatus* (Banks) is known from Madison County, North Carolina and *C. verticalis* is known from Haywood County and Swain County, North Carolina.
- ²³ Kondratieff and Painter (1986) indicated that records of *Hydroperla fugitans* from North Carolina or South Carolina were in error, and that the only confirmed record of this genus was from South Carolina referable to *H. phormidia* Ray and Stark.
- ²⁴ Stark (1985) synonymized *Yugus innubilis* with *Oconoperla weaveri* Stark and Stewart.
- ²⁵ Stark and Szczytko (1982) recognized *Allonarcys* as a synonym of *Pteronarcys*.

Table 2. List of stoneflies (Plecoptera) recorded from North Carolina (NC) and South Carolina (SC). Species marked with an “*” occur in surrounding states and could eventually be collected in either state. New state records for both states as indicated in text are marked by a #.

	NC	SC
Euholognatha		
Capniidae		
<i>Allocapnia aurora</i> Ricker	X	X
* <i>A. brooksi</i> Ross (TN)		
<i>A. fumosa</i> Ross	X	
* <i>A. granulata</i> (Claassen) (TN, VA)		
* <i>A. loshada</i> Ricker (TN, VA)		
* <i>A. mystica</i> Frison (TN, VA)		
<i>A. nivicola</i> (Fitch)	X	
* <i>A. pygmaea</i> (Burmeister) (TN, VA)		
<i>A. recta</i> (Claassen)	X	X
<i>A. rickeri</i> Frison	X	
* <i>A. simmonsii</i> Kondratieff and Voshell (VA)		
<i>A. stannardi</i> Ross	X	
<i>A. virginiana</i> Frison	X	X
<i>A. wrayi</i> Ross	X	X
<i>Nemocapnia carolina</i> Banks	X	X
<i>Paracapnia angulata</i> Hanson	X	
Leuctridae		
<i>Leuctra alexanderi</i> Hanson	X	X
<i>L. biloba</i> Claassen	X	
<i>L. carolinensis</i> Claassen	X	X
<i>L. ferruginea</i> (Walker)	X	X
<i>L. grandis</i> Banks	X	
<i>L. mitchellensis</i> Hanson	X	
<i>L. moha</i> Ricker		X
<i>L. monticola</i> Hanson	X	X
<i>L. nephophila</i> Hanson	X	
<i>L. sibleyi</i> Claassen	X	
<i>L. tenuis</i> (Pictet)		X
<i>L. triloba</i> Claassen	X	X
* <i>L. variabilis</i> Hanson (VA)		
<i>Megaleuctra williamsae</i> Hanson	X [#]	X
<i>Paraleuctra sara</i> (Claassen)	X	X
Nemouridae		
* <i>Amphinemura delosa</i> (Ricker) (TN, VA)		
<i>A. nigrutta</i> (Provancher)	X [#]	X
<i>A. wui</i> (Claassen)	X	X

Table 2. Continued.

	NC	SC
* <i>Ostrocerca albidipennis</i> (Walker) (VA)		
* <i>O. complexa</i> (Claassen) (VA)		
* <i>O. prolongata</i> (Claassen) (VA)		
* <i>O. truncata</i> (Claassen) (VA)		
<i>Paranemoura perfecta</i> (Walker)	X	
<i>Prostoia completa</i> (Walker)	X	X
<i>P. similis</i> (Hagen)		X
<i>P. hallasi</i> Kondratieff and Kirchner	X [#]	
<i>Shipsa rotunda</i> (Claassen)	X	X
<i>Soyedina carolinensis</i> (Claassen)	X	
<i>Zapada chila</i> (Ricker)	X	
Taeniopterygidae		
<i>Boltoperla rossi</i> (Frison)	X	
<i>Oemopteryx contorta</i> (Needham and Claassen)	X [#]	
<i>Strophopteryx appalachia</i> Ricker and Ross	X	
<i>S. fasciata</i> (Burmeister)	X	X
<i>S. inaya</i> Ricker and Ross	X	X
<i>S. limata</i> (Frison)	X [#]	
<i>Taenionema atlanticum</i> Ricker and Ross	X	X
<i>Taeniopteryx burksi</i> Ricker and Ross	X	
<i>T. lita</i> Frison	X	X
<i>T. lonicera</i> Ricker and Ross	X	X
<i>T. maura</i> (Pictet)	X	X
<i>T. metequi</i> Ricker and Ross	X	
* <i>T. nelsoni</i> Kondratieff and Kirchner (VA)		
<i>T. parvula</i> Banks	X	X
<i>T. robinae</i> Kondratieff and Kirchner		X
* <i>T. ugola</i> Ricker and Ross (GA, TN, VA)		
Systellognatha		
Chloroperlidae		
<i>Alloperla atlantica</i> Baumann	X	X
<i>A. caudata</i> Frison	X	
<i>A. chloris</i> Frison	X	
<i>A. furcula</i> Surdick		X
<i>A. nanina</i> (Banks)	X	X
<i>A. neglecta</i> Frison	X	
<i>A. usa</i> Ricker	X	X
<i>Haploperla brevis</i> (Banks)	X	X

Table 2. Continued.

	NC	SC
<i>Rasvena terna</i> (Frison)	X	
<i>Suwallia marginata</i> (Banks)	X	
<i>Sweltsa lateralis</i> (Banks)	X	X
<i>S. mediana</i> (Banks)	X	
<i>S. urticae</i> (Ricker)	X	
Peltoperlidae		
* <i>Peltoperla arcuata</i> Needham (TN, VA)		
* <i>P. tarteri</i> Stark and Kondratieff (VA)		
<i>Tallaperla anna</i> (Needham and Smith)	X	X
<i>T. cornelia</i> (Needham and Smith)	X	X
<i>T. elisa</i> Stark		X
<i>T. laurie</i> Ricker	X	X
<i>T. maria</i> Needham and Smith	X	X
<i>Viehoperla ada</i> (Needham and Smith)	X	X
Perlidae		
<i>Acroneuria abnormis</i> (Newman)	X	X
<i>A. arenosa</i> (Pictet)	X	X
<i>A. arida</i> (Hagen)	X	
<i>A. carolinensis</i> (Banks)	X	X
<i>A. evoluta</i> Klapalek	X	
<i>A. filicis</i> Frison		X
<i>A. frisoni</i> Stark and Brown	X [#]	
* <i>A. internata</i> (Walker) (GA, VA)		
<i>A. lycorias</i> (Newman)	X [#]	
* <i>A. petersi</i> Stark and Gaufin (GA, TN)		
<i>Agnetina annulipes</i> (Hagen)		X
* <i>A. capitata</i> (Pictet) (VA)		
<i>A. flavescens</i> (Walsh)	X [#]	X
<i>Attaneuria ruralis</i> (Hagen)	X	X
<i>Beloneuria georgiana</i> (Banks)	X	
<i>B. stewarti</i> Stark and Szczytko	X	X
<i>Eccoptura xanthenes</i> (Newman)	X	X
<i>Hansonoperla appalachia</i> Nelson		X
<i>Neoperla carlsoni</i> Stark and Baumann		X
* <i>N. catharae</i> Stark and Baumann (TN, VA)		
<i>N. clymene</i> (Newman)	X [#]	
<i>N. occipitalis</i> (Pictet)		X
* <i>N. stewarti</i> Stark and Baumann (TN, VA)		

Table 2. Continued.

	NC	SC
<i>Paragnetina fumosa</i> (Banks)	X	X
<i>P. ichusa</i> Stark and Szczytko	X	X
<i>P. immarginata</i> (Say)	X	X
<i>P. kansensis</i> (Banks)	X	X
* <i>P. media</i> (Walker) (VA)		
<i>Perlesta frisoni</i> Banks	X	X
<i>P. nelsoni</i> Stark	X	X
<i>P. placida</i> (Hagen)	X	
<i>Perlinella drymo</i> (Newman)	X	X
<i>P. ephyre</i> (Newman)	X	X
<i>P. zwicki</i> Kondratieff, Kirchner and Stewart		X
Perlodidae		
<i>Clioperla clio</i> (Newman)	X	X
<i>Cultus decesus isolatus</i> (Banks)	X	
<i>C. verticalis</i> (Banks)	X	
<i>Diploperla duplicata</i> (Banks)	X	X
<i>D. morgani</i> Kondratieff and Voshell	X	
<i>Helopicus bogaloosa</i> Stark and Ray	X	X
<i>H. subvarians</i> (Banks)	X	X
<i>Hydroperla phormidia</i> Ray and Stark		X
<i>Isogenoides hansonii</i> (Ricker)	X	
<i>I. varians</i> (Walsh)		X
<i>Isoperla bellona</i> Banks	X	
<i>I. bilineata</i> (Say)	X	
<i>I. burksi</i> Frison	X	X [#]
<i>I. cotta</i> Ricker		X
<i>I. davisii</i> James	X [#]	
<i>I. dicala</i> Frison	X [#]	X
<i>I. distincta</i> Nelson	X	X
<i>I. frisoni</i> Illies	X	
<i>I. holochlora</i> (Klapalek)	X	X
<i>I. lata</i> Frison	X [#]	
<i>I. marlynia</i> Needham and Claassen		X
<i>I. namata</i> Frison	X	
<i>I. orata</i> Frison	X	X
<i>I. similis</i> (Hagen)	X	X
<i>I. slossonae</i> (Banks)	X	
<i>I. transmarina</i> (Newman)	X [#]	
<i>Malirekus hastatus</i> (Banks)	X	X
<i>Oconoperla innubila</i> (Needham and Claassen)	X	X

Table 2. Continued.

	NC	SC
<i>Remenus bilobatus</i> (Needham and Claassen)	X	X
<i>Yugus arinus</i> (Frison)	X	X
<i>Y. bulbosus</i> (Frison)	X	X
Pteronarcyidae		
<i>Pteronarcys biloba</i> (Newman)	X	X
<i>P. dorsata</i> (Say)	X [#]	X
<i>P. proteus</i> (Newman)	X	X
<i>P. scotti</i> (Ricker)	X	X

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Seasonality in Cetacean Strandings Along the Coast of North Carolina

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ABSTRACT—Records of stranding provide an index by which the resident status and local migratory patterns of cetaceans can be ascertained, especially along North Carolina's lengthy coastline, which extends well into the Atlantic Ocean. Stranding records from North Carolina were compiled by month for all cetaceans to test for seasonal trends. Twenty-six cetacean species have stranded, or come ashore intentionally or unintentionally, along the North Carolina coast, 17 of which are year-round residents. The northern right whale (*Eubalaena glacialis*), fin whale (*Balaenoptera physalus*), humpback whale (*Megaptera novaeangliae*), and harbor porpoise (*Phocoena phocoena*) typically strand during the winter and spring months as they migrate along the North Carolina coast. Although stranding records are available for every month, the bottlenose dolphin (*Tursiops truncatus*) also strands significantly more frequently in winter and spring, which may be explained, in part, by biases inherent in the use of stranding data.

Mammalian diversity in North Carolina exceeds that found in other states and provinces in eastern North America because of the state's extreme physiographic variability (Webster et al. 1985), and marine mammals clearly exemplify this trend. Many species of marine mammals are year-round residents, but others with subtropical and subarctic affinities, such as the West Indian manatee (*Trichechus manatus* Linnaeus) and the harbor porpoise (*Phocoena phocoena* (Linnaeus)), migrate into inshore and nearshore waters during the summer/fall and winter/spring months, respectively. Some closely related taxa that ostensibly occupy the same niche, such as the long-finned pilot whale (*Globicephala melas* (Traill)) and short-finned pilot whale (*G. macrorhynchus* Gray), are thought to be latitudinally parapatric along the state's lengthy (>600 km) coastline, with a dynamic zone of parapatry that shifts relative to the positions of cold-water (Labrador) and warm-water (Gulf Stream) currents.

Stranding data can provide a wealth of biological information about marine mammals (Geraci and St. Aubin 1979). Although the cetacean fauna (whales, dolphins, and porpoises) of North Carolina is relatively well known (Caldwell and Golley 1965, Caldwell and Caldwell 1974, Winn et al. 1979, Schmidly 1981, Lee et al. 1983), there has been no attempt to use the state's stranding records to address the seasonal or distributional ecology of this important component of the marine environment. The purposes of this investigation, therefore, were to describe seasonal periodicity in cetacean strandings in North Carolina and to relate these trends to the zoogeographic significance of North Carolina with regard to the cetacean fauna of the western North Atlantic Ocean.

METHODS

Cetacean stranding data from North Carolina (Schmidly 1981, and references cited therein; Scientific Event Alert Network Bulletins 1975–1982; J. G. Mead, United States National Museum, personal communication) were compiled by month for each species. These references provided a continuous account of strandings reported from the late-1800s through 1990; however, most of the records have been accumulated during the last 20 years after the Marine Mammal Stranding Network was established. Stranding records did not always distinguish between live and dead animals, so both were included in our analysis. It was not possible to verify identifications of all specimens associated with these records, especially those of *Globicephala* and *Stenella* reported in the Scientific Event Alert Network Bulletins and species of small cetaceans reported in newspapers, because voucher material was sometimes not collected (Mead 1977, 1979; Schmidly 1981). Therefore, records were omitted if doubts existed about their veracity. Temporal data were examined statistically (Chi-square) to test the hypothesis that each species exhibited no significant ($P < 0.05$) monthly variation in stranding, although sample sizes were small for some species.

RESULTS AND DISCUSSION

Eight hundred and seventy-two stranding records were available for 26 species of whales, dolphins, and porpoises (Table 1), nine of which exhibit significant monthly variation in their stranding records. Although the bottlenose dolphin (*Tursiops truncatus* (Montagu)) strands in all months of the year, it strands significantly more often in winter and spring. Stranding records for the fin whale (*Balaenoptera physalus* (Linnaeus)) and harbor porpoise (*Phocoena phocoena* (Linnaeus)) display

distinct seasonality, with strandings typically occurring during the winter and spring months. Despite small sample sizes, the northern right whale (*Eubalaena glacialis* (Müller)) and humpback whale (*Megaptera novaeangliae* (Borowski)) also fit into this category. The short-finned pilot whale, long-finned pilot whale, Risso's dolphin (*Grampus griseus* G. Cuvier), Atlantic spotted dolphin (*Stenella frontalis* G. Cuvier), rough-toothed dolphin (*Steno bredanensis* (Lesson)), and dwarf sperm whale (*Kogia simus* (Owen)) display significant monthly variation in stranding without exhibiting well-defined seasonal patterns. Not included in Table 1 are Bryde's whale (*Balaenoptera edeni* Anderson), blue whale (*B. musculus* (Linnaeus)), and short-snouted spinner dolphin (*Stenella clymene* (Gray)), species that have stranded to the north and south of North Carolina but not within state boundaries. Also, the pantropical spinner dolphin (*Stenella attenuata* (Gray)) was not included because we were unable to verify stranding records in North Carolina. These four species probably inhabit state waters seasonally or as occasional strays (Lee et al. 1983, Webster et al. 1985).

Overall, cetaceans strand significantly more frequently during the winter and spring months in North Carolina (Table 1). Several abiotic and biotic factors that are not necessarily related could cause this trend, and examples of each are apparent in these data. Winter storms (known as nor'easters because of the direction from which they blow), coupled with relatively colder water temperatures that slow the process of decomposition, increase the likelihood that a carcass will wash ashore during the winter and spring months. Also, circumstantial evidence suggests that mortality may be greater for some species during the winter and spring months. Finally, certain species of cetaceans are clearly more abundant during the colder months of the year, thus increasing the likelihood of finding stranded animals.

Stranding records for the bottlenose dolphin comprise almost 61% of the total number of cetacean strands reported from North Carolina. Bottlenose dolphin strandings increase during the winter and spring months as local neritic populations are augmented by more northerly inshore and pelagic populations (True 1891, Schmidly 1981, Kenney 1990). Increased winter and spring strandings might simply be an artifact of a larger population during those seasons of the year or mortality rates might be greater during the winter months. Significant stranding increases associated with the dolphin die-off of August–October 1987, when the brevetoxin from the dinoflagellate (*Ptychodiscus brevis*) weakened dolphins such that they contracted lethal secondary bacterial and fungal infection (Geraci 1989), were clearly evident (Fig. 1).

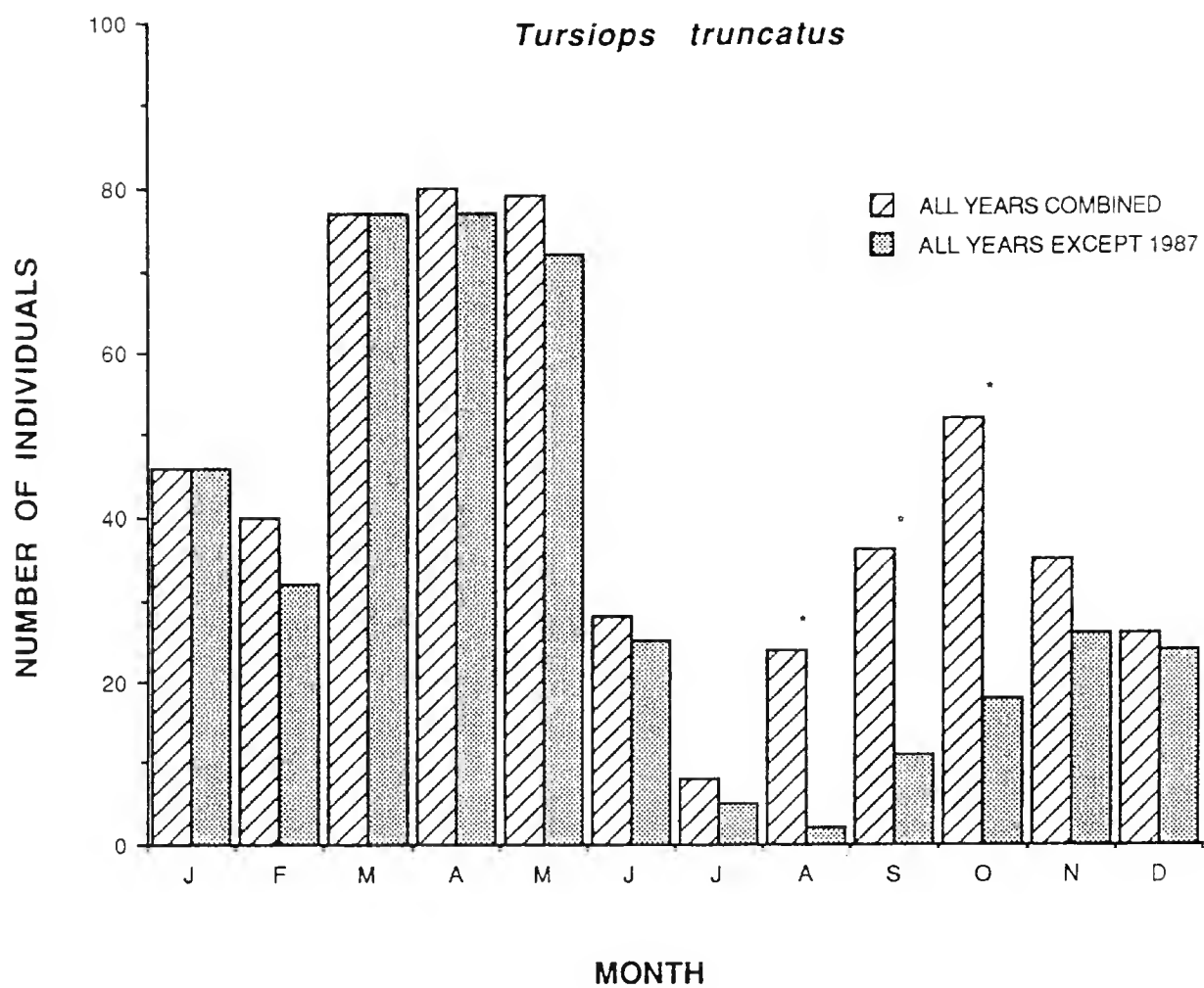


Fig. 1. Monthly stranding records for the bottlenose dolphin (*Tursiops truncatus*) in North Carolina. Significant increases in stranding during the dolphin die-off of 1987 are evident in August, September, and October (*).

FALL/WINTER/SPRING MIGRANTS

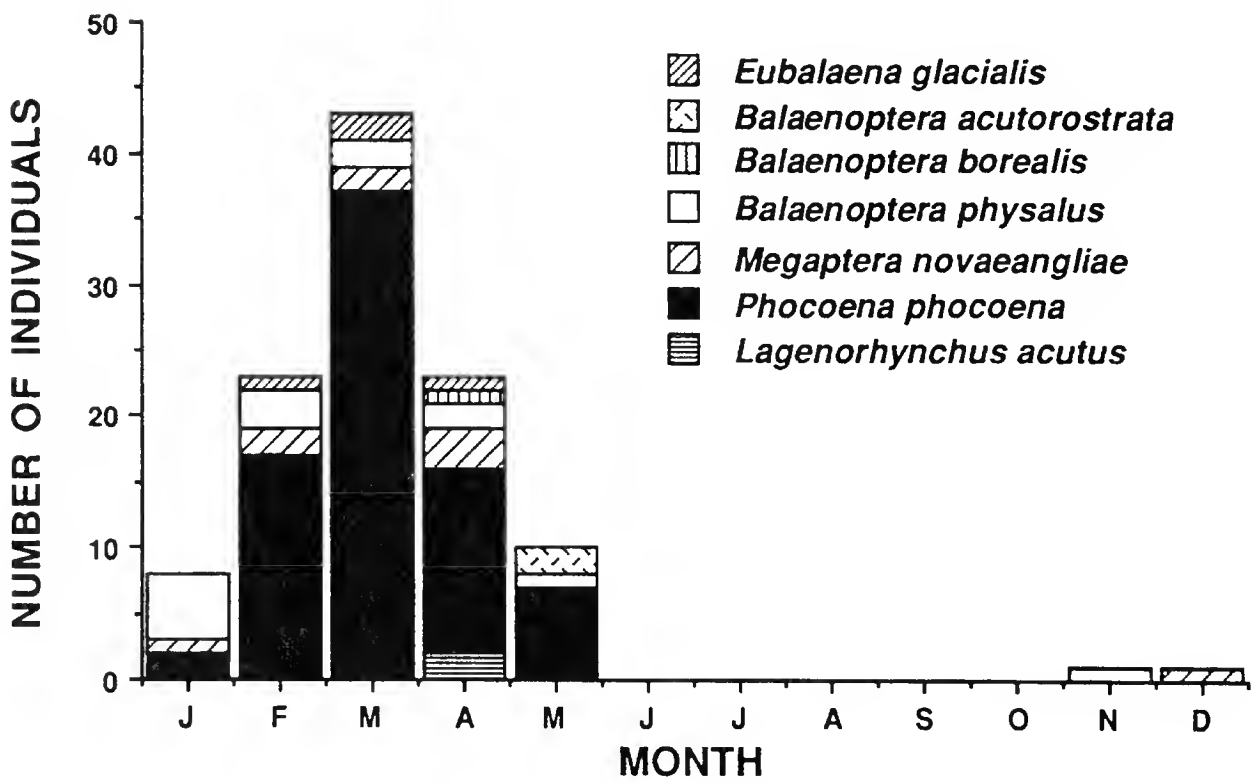


Fig. 2. Monthly stranding records for cetaceans with boreal distributions (see text) that migrate or wander southward along the North Carolina coast during the colder months of the year.

Stranding records for several migratory species such as the northern right whale, fin whale, humpback whale, and harbor porpoise indicate when these species are present along the coast of North Carolina (Fig. 2). These North Atlantic taxa migrate southward during the late fall and winter months, and then return northward in the spring, a pattern best demonstrated by the stranding records for the fin whale and humpback whale. Right whale strandings are confined to the spring months, the season when mothers and their newborn calves migrate northward in shallow nearshore water (Kraus et al. 1986, 1993); the southward winter migration (Reeves et al. 1978) of juveniles, subadults, and adults is farther offshore along the eastern edge of the Labrador Current (Kraus et al. 1993) and the continental shelf (Winn et al. 1986). Stranding records for the harbor porpoise demonstrate a local north-south migration, with the southernmost distributional limits reaching North Carolina during the winter and spring months, rather than the inshore-offshore migratory pattern seen farther north (Neave and Wright 1968, Gaskin et al. 1974, Gaskin and Watson 1985). Based on few stranding records, the sei whale (*Balaenoptera borealis* Lesson) and minke whale (*B. acutorostrata* Lacépède) probably fall into this category as well. These six species account for about 11% of the total number of strandings reported from North Carolina.

The common dolphin (*Delphinus delphis* Linnaeus), striped dolphin (*Stenella coeruleoabla* (Meyen)), sperm whale (*Physeter macrocephalus* Linnaeus), Blainville's beaked whale (*Mesoplodon densirostris* (Blainville)), and Gervais' beaked whale (*M. europaeus* (Gervais)) have stranded during most months of the year, and we suspect that they are year-round residents in North Carolina waters. The common dolphin inhabits temperate waters adjacent to the 100-fathom isobath where the ocean floor has substantial topographic relief (Leatherwood and Reeves 1983). It does not exhibit a pronounced north-south migration, so increased strandings during the colder months may reflect seasonal inshore-offshore movements (Selzer and Payne 1988) or increased mortality during the colder months of the year. Although the sperm whale has a well-documented migration in the North Atlantic Ocean (Townsend 1935), it has stranded in North Carolina in all months except June, October, and December. Mature males migrate northward out of North Carolina waters in the spring, but some immature males and females and their calves remain in North Carolina waters throughout the summer months (Leatherwood et al. 1976). These five species constitute approximately 8% of the total number of strandings reported from North Carolina.

Several cetaceans exhibited significant monthly variation in stranding but demonstrated no seasonal periodicity, and each appears to inhabit

North Carolina waters throughout the year. Monthly variation can be explained by the tendency to mass strand by pilot whales, the rough-toothed dolphin, and possibly Risso's dolphin. It is difficult to explain significant monthly variation exhibited by the Atlantic spotted dophlin (*Stenella frontalis* (G. Cuvier)), which includes stranding records previously attributable to *S. plagiodon* (Cope), a species once thought to inhabit the Atlantic Ocean. Taxonomic uncertainty in the genus and the difficulty in identifying individuals have been presistent sources of error; however, the recent revision of *Stenella* in the western North Atlantic Ocean (Perrin et al. 1987) should help alleviate future misidentifications. Significant monthly variation in stranding by *Kogia simus* might best be explained by a behavior displayed by its close relative, the pygmy sperm whale (*Kogia breviceps* (Blainville)). In southeastern North Carolina, we have noticed that strandings of *K. breviceps* frequently involve females in the process of giving birth or mother-offspring pairs, a behavior also reported by Winn et al. (1979). These seven species account for approximately 17% of the total number of strandings reported from North Carolina.

The remaining seven species of cetaceans are relatively rare in North Carolina waters, and scanty stranding records provide little information about their resident status in the state. The killer whale (*Orcinus orca* (Linnaeus)), false killer whale (*Pseudorca crassidens* (Owens)), True's beaked whale (*Mesoplodon mirus* True), and Cuvier's beaked whale (*Ziphius cavirostris* G. Cuvier) are thought to be year-round residents (Leatherwood and Reeves 1983), but the Atlantic white-sided dolphin (*Lagenorhynchus acutus* (Gray)) inhabits the northern North Atlantic Ocean (Leatherwood and Reeves 1983) and seldom ventures into North Carolina waters. The pygmy killer whale (*Feresa attenuata* Gray) and long-snouted spinner dolphin (*Stenella longirostris* (Gray)) probably enter North Carolina waters during the warmer months of the year (Leatherwood and Reeves 1983). Collectively, this group of species constitutes only about 2% of the total number of strandings reported from North Carolina.

Although marine mammal strandings provide a fortuitous source of information on animals that are not typically accessible, there are inherent biases in conclusions derived from stranding data. Neritic species strand more frequently than pelagic species, so stranding frequencies are less likely to reflect accurately the abundances of pelagic species. Larger-bodied species and mass strandings are more likely to be reported than small-bodied species or single strandings. Also, the Gulf Stream and Labrador Current could transport dead or dying animals beyond their normal ranges and into North Carolina waters.

Conclusions from the North Carolina stranding data, however, agree with information provided by other methods of study for species that are relatively well known.

CONCLUSIONS

North Carolina has the greatest diversity of cetaceans along the east coast of the United States. Twenty-six species have stranded along the North Carolina coast; four other species might inhabit state waters at least seasonally. Based on stranding records, 17 species appear to be year-round residents, although bull sperm whales leave the area during the warmer months. Seven species with boreal affinities migrate or wander southward into the area during the winter and spring months, and two species with austral affinities migrate northward into the area during the summer and fall months. The status of several species needs additional clarification, and as a matter of protocol, voucher material from deceased marine mammals should always be deposited in museum collections to attain that goal.

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Fishes New or Rare on the Atlantic Seaboard of the United States

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ABSTRACT—Sampling over the continental shelf of the South Atlantic Bight, especially off North Carolina, continues to produce records of fishes new to or rare in the area. We document the first records for United States continental shelf water (<200 m depth) of seven fish species: *Cirrhitigaleus asper*, *Symphysanodon berryi*, *Pseudocaranx dentex*, *Lutjanus purpureus*, *Pristipomoides freemani*, *Poecilopsetta beani*, and *Lagocephalus lagocephalus*. In addition, we also report on noteworthy collections of our other fishes captured off North Carolina: *Synagrops spinosus*, *Centropristis fuscus*, *Gonioplectrus hispanus*, and *Etelis oculatus*.

Collections along the Atlantic coast of the Carolinas continue to yield fish species never recorded from the area. Most of these new records represent tropical and subtropical species that extend their published ranges from the Caribbean or the eastern Atlantic (Anderson and Gutherz 1964, Burgess et al. 1979, Böhlke and Ross 1981, Ross

et al. 1981). These additions to the ichthyofauna of the Carolinas are a product of increased scientific collecting efforts in a faunistically-rich region that contains diverse habitats and favorable ocean currents.

During development of the fifth edition of the American Fisheries Society list of common and scientific names of North American fishes (Robins et al. 1991), we supplied records of several species new to North American waters <200 m deep. These data were cited in Robins et al. (1991) as "Rohde (pers. comm.)" or "Rohde et al. (in press)." Since that manuscript was never published, we herein provide validation for the records cited in the American Fisheries Society list, in addition to documentation of several other noteworthy records.

Seven species new to the continental shelf of the United States and four species rare on the Atlantic seaboard are reported. Specimens were collected, often over reef areas, during research cruises using trawls and hook and line, and by intense sampling of the offshore commercial reef fishery where hook and line, and in one instance, a dip net were employed. Museum abbreviations follow Leviton et al. (1985).

SQUALIDAE

Cirrhhigaleus asper (Merrett 1973)

The roughskin dogfish is a widespread continental slope species known from the western North Atlantic, southwest Indian, and central Pacific oceans (Compagno 1984). In the Atlantic it has been recorded from the northern Gulf of Mexico (Compagno 1984) and South Carolina (Castro 1983). We note eight additional western North Atlantic records, including one from North Carolina (the northernmost record): UF 37937 (1, 970 mm TL), Atlantic Ocean off North Carolina (32°38'N, 78°14'W) in 201 m, 8 July 1982; UF 44303 (1, 1000 mm TL), Atlantic Ocean off Georgia (30°52'46"N, 79°46'11"W) in 374 m, 6 November 1985; UF 47509 (1, 920 mm TL), Straits of Florida south of Big Pine Key in 259 m, 3 June 1987; UF 99624 (1, 968 mm TL), Straits of Florida off Big Pine Key, June 1994; UF 38546 (1, 980 mm TL), Gulf of Mexico off Louisiana (27°42'36"N, 93°14'18"W) in 258 m, 10 August 1983; USNM 217364 (1, 1170 mm TL), Gulf of Mexico off Texas (27°42'N, 94°16'W) in 324 m, 12 May 1973; UF 28535 (1, 1144 mm TL), Campeche Bank, Mexico (21°19'30"N, 92°29'W), in 198–225 m, 25 August 1980; and UF 47482 (1, 1000 mm TL), Long Bank off Virgin Islands in 183 m, 4 October 1983.

The advent of deepwater longline and trap fishing has demonstrated that this fish is widely distributed in waters of 183–457 m in the tropical and subtropical western Atlantic. Generic placement of this

species in *Cirrhigaleus*, rather than *Squalus*, follows Shirai (1992) and G. H. Burgess (Florida Museum of Natural History, unpublished data).

ACROPOMATIDAE

Symphysanodon berryi Anderson 1970

The first United States record of the slope bass (UF 38899, 61.3 mm SL) was collected by trawl at 35°07'N, 75°07'W (R/V Albatross IV 82-11, station 23) at a depth of 101-256 m on 16 September 1982. Anderson (1970) reported the species from throughout the Caribbean and the Bahamas in 220-476 m. Although *Symphysanodon* is usually listed as a lutjanid, there is evidence against this placement. It was considered *incertae sedis* but possibly related to the Acropomatidae (especially *Synagrops*) by Johnson (1984), and its taxonomic status is still uncertain (Johnson 1993). Although Eschmeyer (1990) considered it to be in its own family, Symphysanodontidae, Nelson (1994) provisionally placed it in the Acropomatidae.

Synagrops spinosus Schultz 1940

The keelcheek bass has been collected extensively in the Gulf of Mexico in depths >60 m (Hoese and Moore 1977, Potts and Ramsey 1987, Mochizuki and Gultneth 1989, Boschung 1992), and is also known from off Suriname and other Caribbean locations (Fujii 1983, Mochizuki and Gultneth 1989), and from scattered locations in the West Atlantic and West Pacific (Mochizuki and Gultneth 1989). Records of this fish, however, are rare along the United States Atlantic east coast. The following trawl collections document the occurrence of *S. spinosus* on the outer continental shelf (≤ 200 m) of the South Atlantic Bight: UF 41747 (1, 68 mm SL), 35°47'N, 74°53'W in 78 m, 14 July 1980; GMBL-74-92 (1, 61 mm SL), 35°10'N, 75°03'W in 221-229 m, 8 May 1974; GMBL-74-58 (3), 35°02'N, 75°11'W in 238-256 m, 8 May 1974; UF 40027 (1, 114 mm SL), 34°52'N, 75°27'W (Silver Bay station 1283) in 179 m, 17 September 1959 (Bullis and Thompson 1965); UF 39781 (1, 26 mm SL), 34°41'N, 75°37'W (Delaware II 83-5, station 313) in 154 m, 14 May 1983; UF 39898 (1, 73 mm SL), 34°36'N, 75°39'W (Delaware II 83-5, station 315) in 227 m, 15 May 1983; UF 39853 (3, 98, 99, 106 mm SL), 34°18'N, 75°50'W (Delaware II 83-5, station 317) in 379-402 m, 15 May 1983; UF 39816 (4, 55, 49, 49, 48 mm SL), 34°07'N, 76°09'W (Delaware II 83-5, station 323) in 155 m, 16 May 1983; UF 41084 (2, 100, 101 mm SL), 29°49.6'N, 80°10.8'W in 318 m, 29 May 1984; UF 41229 (4, 96, 102, 104, 108 mm SL), 28°40.6'N, 79°53.8'W in 320 m, 31

May 1984; UF 41246 (1, 113 mm SL), 28°29.8'N, 79°50.1'W in 366 m, 31 May 1984.

In addition to the above *S. spinosus* from Silver Bay station 1283, Bullis and Thompson (1965) listed eight other collections (not cited previously) of this species between South Carolina and Cape Canaveral, Florida (82–366 m). Wenner et al. (1979b, c; 1980) also listed several collections of *S. spinosus* from northern Florida to South Carolina (128–338 m). The keelcheek bass seems to be common on the outer continental shelf and upper slope from North Carolina through the Gulf of Mexico and western Caribbean. Many previous records were probably confused with the co-occurring congener *S. bellus* (Goode and Bean). Both species are often collected together, and the most obvious differences between them are the serrations on the anterior edges of the pelvic spines and the second spines of the first dorsal and anal fins of *S. spinosus*. The genus *Synagrops* has been variously placed in the families Apogonidae (Cheilodipteridae) and Percichthyidae (Fraser 1972), but is currently placed in the “oceanic percichthyids,” family Acropomatidae (Johnson 1984).

SERRANIDAE

Centropristis fuscula (Poey 1861)

Four individuals (UF 44997, 50 mm SL, 68 mm SL, 107 mm SL gravid female, 117 mm SL gravid female) of the rare twospot sea bass were taken in a single trawl catch at 33°16'N, 77°13'W (Delaware II 82-04, station 153) at a depth of 97–126 m on 9 July 1982. This trawl appeared to have been pulled mostly over very rough bottom as evidenced by severe net damage and captures of reef organisms (e.g., soft corals). An additional specimen, the largest yet reported, (UF 100391, 168 mm SL gravid female) was captured by hook and line at 32°47'N, 78°11'W at a depth of 165 m on 15 July 1995. These five specimens significantly increase the total known specimens and extend the range northward. Previous records of *C. fuscula* were from Cuba (holotype MCZ 10015, 138 mm SL (Poey 1861); ANSP 94422, 135 mm (Robins and Starck 1961)), Puerto Rico in 183 m (ANSP 144592, 155 mm SL), Gulf of Mexico (1 specimen, G. D. Johnson, United States National Museum, personal communication), and South Carolina (2 collections, listed as *Centropristis* sp. by Wenner et al. (1979a)). The general rarity of specimens and the bottom type of our collection suggest that this species is a cryptic reef fish.

Gonioplectrus hispanus (Cuvier 1828)

The Spanish flag, usually considered a Caribbean insular species,

has been recorded infrequently from scattered locations in the Gulf of Mexico (Bullock and Smith 1991, Boschung 1992) and is also known from the Bahamas through the Caribbean to Brazil (Bullock and Smith 1991, Heemstra and Randall 1993). Until recently, the only record of Spanish flag outside the above distribution was of a single, pelagic larva collected off Cape Fear, North Carolina (Kendall and Fahay 1979). Intensive sampling of the Carolinian snapper/grouper commercial fishery has yielded the following adult specimens, all collected by hook and line over hard bottoms: UF 45042 (208 mm SL), 33°53'N, 76°35'W in 101 m, 1 July 1987; specimen lost (247 mm TL), 33°31.3'N, 76°56.5'W in 40 m, 15 June 1988; specimen sold (250 mm TL), southern Onslow Bay, North Carolina in 46 m, September 1990; UF98891 (gravid female, 182 mm SL), northern Long Bay, North Carolina, 13 November 1991; specimen released, northern Long Bay in 40 m, January 1993; specimen sold (230 mm TL), northern Long Bay in 30 m, July 1993; UF 98892 (gravid female, 180 mm SL), southern Onslow Bay, 15 November 1993; specimen sold (220 mm TL), northern Long Bay in 36 m, January 1994. This species occurs regularly on hard bottoms of the Carolinian outer continental shelf, and the occurrence of both adults (two in spawning condition) and larvae indicates that a reproducing population exists in the South Atlantic Bight.

CARANGIDAE

Pseudocaranx dentex (Bloch and Schneider 1801)

The circumglobal, antitropical range of the white trevally includes the western Indian Ocean, the Indo-West Pacific, the Mediterranean Sea, the eastern Atlantic, mid-Atlantic islands, southern Brazil, and Bermuda (Smith-Vaniz 1984). The first record (UF 42779, 565 mm FL, 526 mm SL) from the United States continental shelf was taken with hook and line off the Carolinas (33°14'N, 77°16'W) on 19 February 1985 in 91 m. Two other large specimens (both marketed) were taken by hook and line: one on 16 November 1985 (835 mm FL) near 33°15'N, 77°24'W in 46–55 m and one on 3 February 1986 (802 mm FL) near 33°06'N, 77°55'W in 49 m. A fourth specimen (ANSP 159577, 785 mm FL) was collected by hook and line in 88 m between 30 July and 5 August 1987 at 33°16.5'N, 77°15'W. One large *P. dentex* was captured (hook and line) and released off the Cape Fear, North Carolina area in 42 m on 3 August 1989. Several of the commercial fishermen recognized this species as different (referring to it as “guelly jack”) and, in addition to the above specimens, they had records of other catches of it from similar areas off Cape Fear. The fisherman who produced the first specimen (above) reported that he had seen *P. dentex*

before, near Matanilla Shoal (northwest end of the Little Bahama Bank).

LUTJANIDAE

Etelis oculatus (Valenciennes 1828)

A single adult specimen of the queen snapper (UF 42778, 673 mm SL) was collected with hook and line 135 km south of Southport, North Carolina at a depth of 201 m on 11 March 1985. Two other adults were landed (not saved) from northern Long Bay, North Carolina: one (915 mm TL) from 219 m in April 1989 and one (685 mm TL) from 164 m in March 1993. These are the first adults of *E. oculatus* recorded north of Florida. Two other small juvenile specimens are known from off the Carolinas (44 mm SL (Anderson and Fourmanoir 1975) and 30 mm FL, South Carolina Marine Resources Monitoring, Assessment, and Prediction Program collections, 33°02.7'N, 77°55.5'W, 59 m, 3 September 1976). *Etelis oculatus* ranges in the western Atlantic from North Carolina and Bermuda south through the Gulf of Mexico (Burgess and Branstetter 1985), the Bahamas, the West Indies, and the Caribbean to Brazil (Anderson 1981, Allen 1985).

Lutjanus purpureus Poey 1867

The Caribbean red snapper, mainly a continental shelf species, was previously known only from the Caribbean (Yucatan and Cuba) south through the Antilles to northeastern Brazil (Allen 1985). There has been some question whether it may be synonymous with *L. campechanus* (Poey) (Vergara R. 1978). Our records demonstrate that these two species of red snappers are sympatric at least through the South Atlantic Bight. The South Carolina Marine Resources Monitoring, Assessment, and Prediction Program has collected three specimens by trawl: 320 mm FL, 34°36.4'N, 76°12.8'W in 35 m, 4 May 1974; 30 mm FL, 30°49.7'N, 81°10.7'W in 13 m, 18 August 1974; 40 mm FL, 30°22'N, 81°18.7'W in 12 m, 18 August 1974. The following records of large adults were obtained from the commercial snapper/grouper fishery: 615 mm TL (specimen photographed but lost), 33°31.3'N, 76°56.5'W in 64 m, 15 June 1988; 620 mm TL (specimen sold), northern Long Bay, NC in 54 m, January 1989; 540 mm TL (specimen sold), southern Onslow Bay, NC in 38 m, June 1989; 630 mm TL (specimen sold), southern Onslow Bay in 42 m, August 1989; 610 mm TL (specimen sold), southern Onslow Bay in 42 m, May 1990. The commercial fishermen generally did not recognize that these fish were different from *L. campechanus*; however, we verified the identifications of the specimens marketed at the fish houses. We distinguished these two species of *Lutjanus* by lateral line scale counts and relative body depths

(Vergara R. 1978).

Pristipomoides freemani Anderson 1966

Only two specimens of the yelloweye wenchman have been collected along the continental shelf of North America. The first specimen (GMBL 78-145, 85.7 mm SL) was collected by trawl off the east coast of Florida at 28°58.4'N, 80°04.4'W in 121–113 m on 18 September 1978 (R/V Dolphin DP 78-07) (W. D. Anderson, Jr., Grice Marine Biology Laboratory, personal communication). The second *P. freemani* (GMBL 82-197, 82 mm SL) was collected by trawl at the same North Carolina station as the previously discussed *C. fuscula* (33°16'N, 77°13'W, R/V Delaware II 82-04, station 153) at a depth of 99 m on 9 July 1982. Additionally, Leis and Lee (1994) reported a single larva from off the Florida Keys questionably attributed to this species. The yellow-eye wenchman was previously known from Uruguay to Panama and Barbados (Anderson 1966, 1972; Matsuura 1983) and off Bermuda (60.3 mm SL; 32°09'N, 64°11'W; 24 August 1971; W. D. Anderson, Jr., personal communication).

PLEURONECTIDAE

Poecilopsetta beani (Goode 1881)

This small flounder, called deep-water dab or offshore flounder (Bigelow and Schroeder 1953, Potts and Ramsey 1987), has been reported from water >200 m deep along the United States continental slope from off New York through the northern Gulf of Mexico to Campeche (Goode and Bean 1896, Tyler 1960). Its distribution south of Mexico has been inconsistently reported: from off northern Colombia and St. Kitts, Lesser Antilles (Goode and Bean 1896), possibly to the greater Antilles (Tyler 1960), and from off northern Brazil (Topp and Hoff 1972). In addition to the southernmost Brazilian record, Bullis and Thompson (1965) list several collections from deep water along the Central American coast. We have two records of *P. beani* from off North Carolina collected by trawl during the same cruise (Delaware II 83-05). The first specimen (UF 39809, 18 mm SL) represents the first report of this species shallower than 200 m and was collected at 34°07'N, 76°09'W in 155 m (station 323) on 16 May 1983. The second specimen (UF 39891, 56 mm SL) was collected at 34°36'N, 75°39'W in 227 m (station 315) on 16 May 1983. Two larval specimens (MCZ 78481 and 78491, *Poecilopsetta* sp.), probably *P. beani*, have also been collected off North Carolina. This species was not included in the most recent American Fisheries Society list of common and scientific names of North American fishes (Robins et al. 1991), but

based on the above record (UF 39809), it should be added to the continental shelf fauna.

TETRAODONTIDAE

Lagocephalus lagocephalus (Linnaeus 1758)

The first United States oceanic puffers (UF 44194, 169 mm SL; 190 mm SL, specimen mounted) were collected at 34°21.5'N, 75°55'W in 64 m on 6 August 1985. They were dipnetted at night from a school of 6 to 8 individuals swimming at the surface. *Lagocephalus lagocephalus* is widespread, ranging through the eastern Atlantic, the Mediterranean Sea, and the Pacific and Indian oceans (Shipp 1974). Templeman (1962) reported the first North American occurrence of the species from a single individual collected in Newfoundland. Other isolated western Atlantic records of the species include Bermuda, the Gulf Stream off Florida, and Curacao (Shipp 1974).

DISCUSSION

The offshore (>20 m) ichthyofauna of North Carolina, particularly on hard bottoms, is dominated (species numbers) by tropical and subtropical species. Expanded sampling of the offshore hard bottom and outer shelf habitats continues to increase the number of these forms known off the Carolinas. Although the Gulf Stream undoubtedly helps disperse tropical organisms into the area, many of these southern species apparently maintain self-sustaining populations on North Carolina's middle to outer continental shelf (Grimes et al. 1977, Grimes and Huntsman 1980, S. W. Ross, North Carolina National Estuarine Research Reserve, unpublished data). Burgess et al. (1994), in fact, proposed that a redefined tropical West Indian zoogeographic province should include the reefs of the outer continental shelf of the South Atlantic Bight to Cape Hatteras. The 11 species documented herein are most common in warm-temperate to tropical waters along the outer shelf or upper slope south of North Carolina. Three of these (*C. fuscus*, *G. hispanus*, *L. purpureus*) tend to be benthic and tied to reef-like habitats. The remainder are either pelagic or benthopelagic, and are capable of extensive movements.

Briggs (1974) noted that, within the warm-temperate Carolinian Region, the northern Gulf of Mexico contained a richer fish fauna (375–400 species) than the Atlantic coast. Since his publication, many new records have been added to both areas. Hoese and Moore (1977) reported over 400 fishes from the northern Gulf of Mexico, and Boschung (1992) listed around 663 marine fishes from the eastcentral Gulf of Mexico. Dahlberg (1975) reported nearly 400 species in and near Georgia

coastal waters. With the additions reported herein, the North Carolina marine ichthyofauna in less than 200 m contains over 680 species (S. W. Ross and G. H. Burgess, unpublished manuscript). However, many of these are cold-temperate species that rarely range south of Cape Hatteras, and thus, are not permanent members of the Carolinian Region. The North Carolina ichthyofauna is much richer than previously reported, and future zoogeographic and systematic data will likely prove that the northern Gulf of Mexico and the South Atlantic Bight are not significantly different in fish species richness.

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A New Species of Crayfish of the Genus *Orconectes*,
Subgenus *Procericambarus* (Decapoda: Cambaridae),
Endemic to the Neuse and Tar-Pamlico River Basins,
North Carolina

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ABSTRACT—*Orconectes (Procericambarus) carolinensis* is a new species in the Spinosus Group, and the only member of its subgenus known from east of the Blue Ridge physiographic province. It is endemic to the Neuse and Tar-Pamlico river basins of North Carolina, where it occurs in the Coastal Plain and the eastern edge of the Piedmont Plateau. It is most closely related to *O. (P.) spinosus* and *O. (P.) putnami*, but may be distinguished from these and other members of the Spinosus Group by: the greater length of the terminal elements of the form I male gonopod (first pleopod); the shorter and broader areola; the somewhat longer acumen and rostrum; the occasional presence of multiple cervical spines and small spiniform hepatic tubercles; the smaller size; and various aspects of tuberculation and spination of the palm, dactyl, merus, and ischium of the cheliped. The species is probably derived from an ancestral *Procericambarus* stock that inhabited the Tennessee and Teays river basins, gained access to the Atlantic versant following a breach of the Blue Ridge by headwaters of the young Roanoke River, and later entered the Greater Pamlico River from the Greater Roanoke by stream captures.

The Neuse and Tar-Pamlico rivers rise in the eastern Piedmont Plateau of North Carolina, flow southeast across the Coastal Plain of the state, and debouch at saline estuaries of Pamlico Sound on the Atlantic coast. Throughout their lengths they are parallel riparian systems that support nearly identical faunas and, although now separated, during much of the Pleistocene they undoubtedly were a

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single hydrologic unit, the Greater Pamlico River (Lachner and Jenkins 1971:62). Particularly notable in the Neuse and Tar-Pamlico faunas are a number of disjunct endemic species that exhibit closest affinities with congeners whose ranges lie well beyond the two North Carolina rivers.

The endemic fish, *Noturus (Rabida) furiosus* Jordan and Meek, is widespread in both rivers, as are its more broadly distributed congeners, *Noturus (Schilbeodes) gyrinus* (Mitchill) and *Noturus (Schilbeodes) insignis* (Richardson). As interpreted by Taylor (1969), however, the closest relatives of *N. furiosus* are *Noturus (Rabida) munitus* Suttkus and Taylor, *Noturus (Rabida) placidus* Taylor, and *Noturus (Rabida) stigmosus* Taylor, which, along with *N. furiosus*, comprise the “*furiosus* group.” Geographically, the nearest of the three western relatives of *N. furiosus* is *N. munitus*, which occurs in the Conasauga River of southeastern Tennessee and in the Pearl, Tombigbee, and Cahaba rivers of Alabama, Louisiana, and Mississippi (see Rohde 1980 for distribution maps).

The large, branchiate salamander, *Necturus lewisi* (Brimley), is also endemic and widespread in the Neuse and Tar-Pamlico rivers (Braswell and Ashton 1985). Its closest relative is considered to be the sympatric but wider ranging *Necturus punctatus* (Gibbes) (Ashton et al. 1980; Sessions and Wiley 1985), which inhabits the Atlantic Coastal Plain from southeastern Virginia to central Georgia. The ranges of these two species, although overlapping in the Neuse and Tar-Pamlico basins, are broadly disjunct from those of the other *Necturus* species. *Necturus maculosus* (Rafinesque) is the only other member of the genus that occurs in North Carolina, where it appears to be limited to the French Broad River basin in the Blue Ridge (Martof et al. 1980:50).

The ranges of several invertebrates exhibit the same phenomenon. The unionid mollusk, *Elliptio (Canthyria) steinstansana* Johnson and Clarke, is endemic to the Tar-Pamlico River, but its nearest relatives occur in the James River basin to the north and the Altamaha River basin to the south. Among the eight species of crayfishes known to occur in the Neuse and Tar-Pamlico rivers (Cooper and Ashton 1985:9–10) are two endemic species, *Procambarus (Ortmannicus) medialis* Hobbs, and the species of *Orconectes* described herein. *Procambarus medialis* is most closely related to two other Coastal Plain members of the Planirostris Group in North Carolina: *Procambarus (Ortmannicus) plumimanus* Hobbs and Walton, of the Northeast Cape Fear and New (White Oak) basins (Cooper and Braswell 1995), and *Procambarus (Ortmannicus) pearsei* (Creaser), of the Cape Fear, Waccamaw, and

Lumber-Little Pee Dee basins. These three species of very limited distribution constitute a “disjunct enclave” whose nearest relatives—*Procambarus* (*Ortmannicus*) *hybus* Hobbs and Walton, *Procambarus* (*Ortmannicus*) *mancus* Hobbs and Walton, and *Procambarus* (*Ortmannicus*) *planirostris* Penn—inhabit elements of the Gulf drainage in Alabama, Mississippi, and the Florida Parishes of Louisiana (Hobbs and Walton 1958:11; Hobbs 1975:15).

The new species of *Orconectes* described below is yet another Neuse and Tar-Pamlico endemic whose range is widely disjunct from the ranges of its closest relatives. It “is only the third, and southernmost, species of *Orconectes* recorded from anywhere on the Atlantic seaboard” (Cooper and Cooper 1977:199), and has its closest affinities with species found in and west of the Blue Ridge rather than with its geographically close congener, *Orconectes* (*Crockerinus*) *virginiensis* Hobbs, of southeastern Virginia and northeastern North Carolina.

First reports of an *Orconectes* in the Tar-Pamlico River appeared in the late 19th and early 20th centuries, but the animal was assigned to Bundy’s *Cambarus* (= *Orconectes*) *spinosus* (Bundy 1877; Faxon 1884, 1890; Harris 1903; Ortmann 1905, 1931), a creature of the Tennessee and Coosa river basins. Bundy’s specimens, which came from the Tar River at Rocky Mount, Edgecombe County, apparently were the only ones on which the several subsequent reports were based. Later papers (e.g., Hobbs 1972, 1974, 1989; Hobbs and Peters 1977) did not comment on an *Orconectes* in this Atlantic drainage river, although Hobbs (1981:294) repeated Ortmann’s (1931) statements (based on Faxon) that “*C. spinosus*” occurred in the Tar River.

Over 200 specimens of this crayfish, from 43 localities, have now been collected. Examination of this material verifies our opinion that the animal is quite distinct from other members of the genus *Orconectes*.

Orconectes (*Procericambarus*) *carolinensis*, new species

Figure 1

Cambarus spinosus Bundy.—Faxon, 1890:632 [p.p.: “Tar River Rocky Mount, North Carolina.”].—Harris, 1903:180 [p.p.: “North Carolina. 1. Tar River, Rocky Mount (Nash County). F., ’90”].—Ortmann, 1905:115 [p.p.: “Atlantic drainage ... North Carolina”].—Hobbs, 1981:294 [p.p.: quoting Ortmann 1905].

C. spinosus Bundy.—Ortmann, 1931:87 [p.p.: “Tar River, Rocky Mount, Edgecombe Co., North Carolina, according to Faxon”], 88 [p.p.: “(from ... North ... Carolina)” ...].—Hobbs, 1981:294 [p.p.: quoting Ortmann, 1931:87].

“recently discovered species of *Orconectes* ...”.—Cooper and Cooper, 1977:199.

Orconectes sp. A.—Cooper and Ashton, 1985:9.—Cooper and Braswell, 1995:88, 89, 123, 126.

Diagnosis—Body and eyes pigmented, eyes large. Rostrum acarinate, deeply excavate, with conspicuous acumen, delimited basally on each side by strong, acute marginal spine; margins of rostrum thickened, elevated, parallel from base to marginal spines; acumen 42.6 to 57.3 (\bar{x} = 50.1, n = 113) percent length of rostrum. Areola 3.0 to 5.8 (\bar{x} = 4.2, n = 112) times longer than wide, constituting 25.5 to 31.1 (\bar{x} = 28.5, n = 113) percent of total carapace length (TCL) and 39.0 to 43.3 (\bar{x} = 41.2, n = 113) percent of postorbital carapace length (PCL), with 4 to 8 (mode 6) punctations across narrowest part. Cervical spines long, acute, usually single spine each side of carapace (70.7% of 123 specimens). Branchiostegal spine prominent, acute; hepatic spines or spiniform tubercles only occasionally present. Suborbital angle vestigial to nearly obsolete; postorbital ridge well developed, with prominent cephalic spine. Antennal scale 2.7 to 3.6 (\bar{x} = 3.1, n = 113) times as long as broad, widest just distal to midlength, lateral margin thickened and terminating cephalically in long spine. Palm of chela inflated (ratio width to depth 1.4–1.8, \bar{x} = 1.6, n = 108), lateral margin costate for most of length; dorsal surfaces of palm and fingers usually with dense setae; mesial margin of palm with 2 rows of tubercles, mesialmost row subserrate, with 6 to 11 (mode 7–8) prominent, acute tubercles; irregular row of 4 to 10 (mode 7–8) smaller, truncate or subsquamous (but often acute) tubercles subtending mesial row dorsally; conspicuous tuft of setae at opposable bases of both fingers; fixed finger with well defined ridges dorsally, mildly costate dorsolaterally; opposable surface of finger with row of 4 to 8 (mode 5–6) knoblike tubercles between base and about midlength of finger, and isolated subconical tubercle ventral to continuous row of denticles at base of distal one-third or one-fourth; opposable surface of dactyl moderately excised in basal one-third in adult males; dactyl with well defined dorsal ridges flanked by rows of setiferous punctations; proximal one-half to two-thirds of mesial margin of dactyl with 2 rows of prominent tubercles, ventral row often subserrate in dorsal outline, with 4 to 10 (mode 6) somewhat depressed, often spiniform tubercles; dorsal row with 3 to 8 (mode 4) tubercles, and sometimes subtended laterally by third short, irregular row; opposable surface of dactyl with row of 4 to 9 (mode 6) knoblike tubercles between base and about midlength.

Merus of cheliped with at least 2 long subdistal spines dorsally, and 1 to 4 short, acute spines proximal to them; ventromesial ridge

of merus with longitudinal row of 2 to 8 (mode 4–5) prominent, acute spines in addition to long distal spine, ventrolateral ridge with longitudinal row of 2 to 7 (mode 2–3) prominent, acute spines in addition to long distal spine. Ventral surface of carpus of cheliped almost always with strong distomedian spine, and larger acute spine on lateral articular condyle; mesial surface of carpus with long, procurved spine at about midlength, usually smaller spine distal to it, and tubercle, often spiniform, near proximal margin.

Hook on ischium of third pereopod of form I male usually extending beyond basioischial articulation, sometimes opposed by low, vestigial tubercle on basis. Length of gonopod (first pleopod) of form I male divisible into TCL 2.1 to 2.5 ($\bar{x} = 2.2$, $n = 54$) times; cephalic surface of gonopod with prominent angular shoulder, distal to which both rami inclined cephalically; terminal elements long, slender, subparallel to about midlength of mesial process; central projection tapering smoothly from base to acute tip, distal portion gently recurved, tip directed caudodistally and reaching to or beyond midlength of coxa of first pereopod when abdomen flexed; length of central projection 46.5 to 57.9 ($\bar{x} = 51.6$, $n = 54$) percent of total length of gonopod; tip of mesial process somewhat spatulate and mildly excavate cephalically; length of mesial process 34.7 to 44.5 ($\bar{x} = 41.5$, $n = 54$) percent of total length of gonopod, and 73.3 to 89.2 ($\bar{x} = 80.4$, $n = 54$) percent of length of central projection. In caudal (ventral) aspect, bases of gonopods and tips of mesial processes contiguous; tip of central projection directed slightly distolaterally, that of mesial process directed distomesially.

Annulus ventralis inflexibly fused to sternum; annulus 1.3 to 1.4 times wider than long, with deep, broad transverse fossa; cephalic border of annulus convex, caudal border subangular; cephalomedian wall with short longitudinal trough, flanked at each side by ridge, ridges diverging caudally and each terminating in large, rounded cephalolateral prominence, prominences in ventral aspect obscuring cephalic half or more of fossa; caudomedian wall dissected by sinus; obvious sulcus cephalic to caudal margins.

Measurements of type specimens provided in Table 1.

Holotypic male, form I—Body and eyes pigmented, eye 2.5 mm diam. Cephalothorax (Fig. 1A, D) subcylindrical, somewhat depressed dorsally; carapace widest at midlength, width greater than depth at caudodorsal margin of cervical groove; abdomen narrower than carapace. Areola 4.1 times longer than wide, constituting 29.5 percent of TCL (42.0% of PCL), with 5 punctations across narrowest part and low, rounded eminence at caudal base. Rostrum acarinate, length 31.2 percent of TCL (44.4% of PCL), deeply excavate, with thickened, elevated

Table 1. Measurements (mm) of types, *Orconectes (P.) carolinensis*, new species.

	Holotype	Allotype	Morphotype
Carapace			
Total length	29.2	29.7	23.9
Postorbital length	20.5	20.9	17.1
Width	14.1	14.0	10.9
Depth	11.4	12.7	9.8
Rostrum			
Length	9.1	9.3	7.3
Width at base	4.2	4.4	3.7
Length acumen	4.4	4.5	3.5
Areola			
Length	8.6	9.1	7.1
Width	2.1	2.3	1.7
Antennal scale			
Length	7.8	8.2	6.6
Width	2.5	2.8	2.3
Abdomen			
Length	33.5	34.7	27.1
Width	10.9	11.5	9.0
Cheliped (right)			
Length lateral margin chela	24.5	17.6	16.7 *
Length mesial margin palm	7.2	5.7	5.1 *
Width palm	9.2	7.0	6.3 *
Depth palm	5.6	4.4	3.7 *
Length dactyl	13.7	9.5	9.1 *
Length carpus	7.9	7.3	5.9
Width carpus	5.4	4.7	4.3
Depth carpus	4.7	4.0	3.3
Length dorsal margin merus	10.7	9.3	7.8
Depth merus	5.0	5.1	4.1
Gonopod length	13.1	NA	10.5

* Left chela.

margins bearing long marginal spine at base of acumen each side; rostrum subrectangular, margins converging very slightly to base of marginal spines; walls and floor of rostrum with setose punctations, proximal portion of floor cephalodorsally acclivous, floor of acumen plane. Acumen length 48.4 percent of rostrum length, strongly tapering from base to acute, corneous tip, which extending to distal margin of second article of antennular flagellum. Subrostral ridge strong, evident in dorsal aspect from base of rostrum to marginal spines.

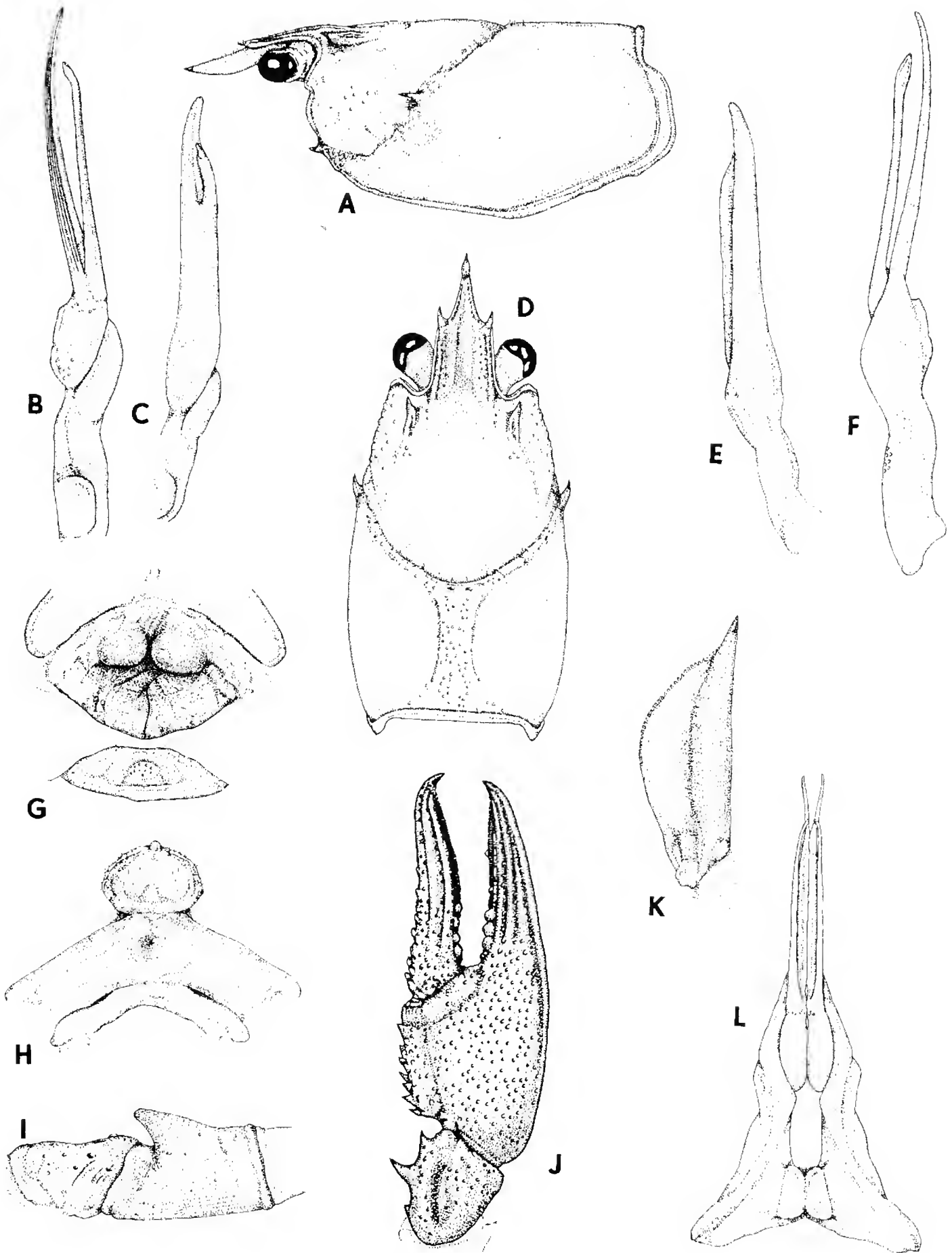


Fig. 1. *Orconectes (Procericambarus) carolinensis*, new species (all from holotypic male, form I, except C, E, from morphotypic male, form II, and G, from allotypic female; setae not illustrated): A, lateral aspect of carapace; B, C, mesial aspect of gonopod (first pleopod); D, dorsal aspect of carapace; E, F, lateral aspect of gonopod; G, annulus ventralis and postannular sclerite; H, epistome; I, basal podomeres of third pereopod; J, dorsal aspect of distal podomeres of cheliped; K, antennal scale; L, caudal aspect of in situ gonopods.

Postorbital ridge strong throughout most of length, with shallow, setiferous dorsolateral groove; cephalic margin terminating in strong spine. Suborbital angle nearly obsolete, delimited ventrally by shallow rounded notch at proximal base of antennal peduncle. Cervical spines strong, acute, directed cephalolaterally, 1 each side, plus single, small spiniform tubercle just dorsal to spine. Branchiostegal spine prominent, acute. Hepatic region punctate, with some small subspiniform tubercles. Carapace densely punctate dorsally (including gastric region) and laterally, somewhat granulate ventrolaterally; cluster of tubercles just caudal to branchiostegal spine and ventral to cephalolateral portion of cervical groove, which with row of tubercles extending along ventral margin; cervical groove deep, uninterrupted, with shallow, curved sulcus (tributary to groove) ventral to cervical spine, creating subglabrous mound below spine.

Abdomen slightly longer than carapace; pleura well developed, subtruncate, with smoothly rounded cephaloventral margins and subangular caudoventral margins; minute atypical notch in apex of second through fourth pleura. Cephalic section of telson with large, acute, immovable spine at caudolateral corner, and smaller, movable spine just mesial to it (that on right side small, regenerate); cephalic and caudal sections of telson partly separated by oblique lateral incisions and shallow transverse sulcus. Proximal podomere of uropod with long, corneous spine on mesial lobe and slightly smaller spine on lateral lobe; mesial ramus of uropod with distolateral marginal spine and relatively broad median keel terminating distally in acute premarginal spine; cephalic section of lateral ramus with median keel terminating in acute spine at transverse flexure, which with total of 13 fixed spines and 1 large movable spine at lateral margin.

Cephalic lobe of epistome (Fig. 1H) spatulate, tilted cephaloventrally, with moderate constriction and deep transverse groove at caudal base; cephalomedian margin with slight notch ventral to short projection; cephalolateral margins elevated (ventrally), broad, sloping onto ventral surface and with thin, emarginate rim bearing short setae; lateralmost extremities mildly flanged; ventral surface of lobe concave, punctate, with short, sparse setae, concavity continuing into cephalomedian notch; caudal one-third of ventral surface with low, subtriangular eminence; main body of epistome relatively glabrous, cephalomedian and cephalolateral margins forming a somewhat hemitubular, curved ridge; central depression of body broad, deep, with deep fovea situated in midline at cephalic margin of depression; zygoma moderately arched, wider than space between renal apertures; pits at cephalolateral borders of zygoma elongate and relatively shallow.

Proximal podomere of antennular peduncle with strong spine on ventral surface slightly proximal to midlength; antennal peduncle with acute ventromedial spine on ischium and larger distolateral spine on basis. Antennal flagellum about 49 mm long, tip reaching midlength of fourth abdominal tergite when flagellum adpressed. Antennal scale (Fig. 1K) 3.1 times as long as wide, greatest width just distal to midlength; distal margin of lamella steeply declivous to widest part, row of setae not encroaching on base of apical spine, mesial margin narrowly curved; lateral margin thickened, gently bowed and with strong apical spine, tip of which directed distolaterally and reaching distal margin of ultimate podomere of antennular peduncle and base of distal one-third of same podomere of antennal peduncle.

Third maxilliped with tip reaching about midlength of basal podomere of antennal peduncle, tip of exopodite reaching base of distal one-fourth of merus of endopodite; cephalolateral margin of ischium produced as acute spine; ventrolateral ridge flanked mesially by row of punctations bearing short setae; most of ventrolateral half with sparse punctations and short setae, but distomedial margin with longer setae; ventromesial half of ischium with long, stiff setae, longer and more dense proximally than distally and obscuring proximal portion; surface between bases of setae and dentate mesial margin glabrous, margin with 23 denticles. Right mandible with incisor ridge bearing 7 denticles (6 on left).

Right chela (Fig. 1J) with moderately inflated palm, ratio width to depth 1.6, ratio length to depth 1.3; lateral margin of palm and proximal fixed finger visibly but narrowly costate dorsally and ventrally; chela 2.7 times longer than wide, shorter than carapace (ratio TCL to chela length 1.2). Dorsal surface of palm densely punctate, most punctations with short setae, but longer and more plumose ones laterally and mesially. Mesial margin of palm with 2 obvious rows of tubercles; mesialmost row subserrate, with 8 acute, subconical tubercles (9 on left chela), and distomesial margin of articular ridge produced as additional rounded tubercle; single small, rounded tubercle at proximolateral base of proximalmost tubercle; mesial row of tubercles flanked dorsally by irregular row of 7 (8 on left) anteriorly rounded to subsquamous tubercles; 2 rounded tubercles dorsal to dorsal row at about midlength of palm, and 4 subsquamous to squamous tubercles lateral to these; all tubercles with group of setae originating at distal base. Ventral surface of palm subglabrous, with sparse, shallow punctations and minute setae.

Fingers moderately gaping in proximal half, opposable surfaces contiguous along distal half. Dactyl subovate in cross-section; mesial surface gently bowed, with 2 rows of anteriorly elevated and rounded

tubercles, somewhat subserrate in dorsal outline; 10 tubercles (13 on left dactyl) in ventromesial row, extending to base of distal two-fifths of finger; single tubercle proximovernal to first in ventromesial row (on left, similar tubercle ventral to first); dorsomesial row with 6 tubercles (7 on left); single small, rounded tubercle dorsal to base of first one in dorsomesial row. Ventral surface of dactyl rounded, with sparse punctations bearing setae. Opposable surface of dactyl with mat of plumose setae at base, and moderate excision extending from first to fourth tubercles; margin with row of 9 knoblike tubercles; denticles in 3 to 4 rows, extending along distal two-thirds of finger.

Fixed finger of propodus subtriangular in cross-section, with well developed, fairly broad middorsal ridge, which essentially glabrous, but with sparse punctations on proximal one-fifth; ridge mesially and laterally subtended by groove containing row of setiferous punctations extending nearly to base of tip, and flanked each side by somewhat abbreviated ridge, ridges merging at about base of distal one-fourth of finger; rudimentary dorsolateral ridge in proximal half of finger, extending to about midlength; lateral margin proximally costate. Opposable surface of fixed finger with setae at base, margin with row of 8 knoblike tubercles extending to about midlength; subconical tubercle at base of distal one-third of finger, ventral to denticles, which in 3 to 4 continuous rows.

Right carpus (Fig. 1J) 1.5 times as long as wide, 1.7 times as long as deep, ratio width to depth 1.1; carpus punctate dorsally, with oblique median sulcus, several squamous tubercles on dorsomesial surface; mesial surface sparsely punctate, with long procurved spine at midlength, flanked proximally by smaller, somewhat acute tubercle near mesial base of podomere; second long, acute spine situated proximomesial to articular eminence; ventromesial surface with sparse, setiferous punctations and several very small tubercles; ventral surface with large disto-median spine and larger spine on distal end of lateral articular condyle; lateral surface of carpus with scattered setiferous punctations.

Right merus 2.1 times as long as deep; dorsal surface with 2 long subdistal spines; ventromesial ridge with acute distal spine and 5 additional ones, ventrolateral ridge with acute distal spine and 4 additional ones, none on distolateral articular condyle; lateral and mesial surfaces of merus essentially glabrous. Right ischium with row of 3 low, subacute tubercles on ventral ridge, distal to suture line; small hooklike sufflamen adjacent to large articular condyle of coxa.

Palm of chela and carpus of second pereopod with row of long setae on dorsomesial and ventromesial surfaces, no stiff setae on mesial margin; other podomeres with rows of long setae on ventral or ventromesial

surfaces and sparse setae on dorsomesial surface, none stiff; distal margin of merus of second through fourth pereopods with small, acute ventrolateral spine. Coxa of fourth pereopod without boss, ventral surface punctate and with long setae; ventral membrane on coxa of fifth pereopod studded with short setae. Ischium of third pereopod (Fig. 1I) with simple hook extending past basioischial articulation by nearly half its length, hook opposed by vestigial tubercle on basis. Gonopods (Fig. 1B, F, L) symmetrical (see "Diagnosis" for description). In addition, left gonopod length 44.9 percent of TCL (63.9% of PCL).

Allotypic female—Differing from holotype in following respects: areola 4.0 times as long as wide, length 30.6 percent of TCL (43.5% of PCL). Tip of acumen extending to midlength of second article of antennular flagellum. Small acute tubercle ventrocephalic to cervical spine. Total carapace length 85.6 percent of abdomen length. Antennal scale 2.9 times longer than wide, tip of apical spine extending to about midlength of second article of antennular flagellum. Palm of right chela 1.6 times wider than deep; chela much shorter than carapace (ratio chela length to TCL 1.7), and 2.5 times longer than wide; mesial row of tubercles on palm subtended dorsally by irregular row of 6 tubercles. Mesial surface of dactyl not bowed, opposable base not excised, closed fingers without proximal gape. Mesial surface of dactyl with ventromesial row of 4 acute but depressed tubercles. Opposable surface of fixed finger with row of 6 (5 on left) knoblike tubercles extending just distal to midlength of finger; subconical ventral tubercle situated just proximal to base of distal one-third of finger. Right carpus 1.8 times as long as deep, ratio width to depth 1.2. Right merus 1.8 times longer than deep. Right ischium with row of 4 acute tubercles on ventral ridge.

Annulus ventralis (Fig. 1G) as described in "Diagnosis." In addition, first pleopod well developed, extending beyond cephalic margin of annulus when abdomen flexed. Postannular sclerite (Fig. 1G) 3.2 times wider (2.9 mm) than long (0.9 mm).

Morphotypic male, form II—Differing from holotype in following respects: rostrum 30.5 percent of TCL (42.7% of PCL); acumen length 47.9 percent of rostrum length. Total carapace length 88.2 percent of abdomen length. Left chela (right regenerate) 2.7 times longer than wide; mesial margin of palm with subserrate mesial row of 7 spiniform tubercles, distal margin developed as eighth. Mesial surface of dactyl with subserrate row of 6 acute tubercles extending to about midlength of finger, dorsally subtended by irregular row of 5 squamous tubercles and ventrally by several squamous tubercles; opposable surface of dactyl with 4 knoblike tubercles extending to about base of distal

one-third of finger, fourth slightly offset ventrally, small vestigial fifth tubercle dorsal to row of denticles just distal to fourth tubercle, another small tubercle interrupting denticles just proximal to midlength of finger, and a minute, conical tubercle (smaller than denticles and among them) distal to midlength. Opposable surface of fixed finger with 4 knoblike tubercles, smaller fifth tubercle at about midlength of finger. Antennal scale 2.9 times longer than wide. Tip of antennal flagellum reaching nearly to caudal margin of third abdominal tergite. Merus with 3 spines each on ventrolateral and ventromesial ridges. Hook on ischium of third pereopod greatly reduced.

Left gonopod (Fig. 1C, E) somewhat aberrant, mesial process in mesial aspect slightly longer than on right, tip curving cephalically, recurving, directed distocephally; terminal elements of gonopod shorter and more robust, both less acute, central projection not corneous, cleft between terminal elements much shorter; cephalic border of gonopod without prominent angular shoulder. Right gonopod 43.9 percent of TCL (61.4% of PCL).

Color notes—Base color varies from tan to forest green. Dark brown to black saddle, often mottled, on posterior carapace, narrowest between caudal bases of branchiocardiac grooves and caudal ridge; horns of saddle produced along ventrolateral margin of carapace as far cephalically as anteroventral branchiostegal region below spine; anterolateral branchiostegite with somewhat reticulated blotches of brown, olivaceous, or black pigment; antennal region of carapace cream; mandibular adductor region with irregular dark brown to black splotches or mottlings; tips of acumen and marginal, cephalic, and cervical spines crimson or orange, subtended proximally by black band; marginal ridges of rostrum black; most of carapace and abdomen with fine dark flecking. Cephalic portion of first abdominal segment with paired, subtriangular, dorsolateral blotches, dark brown, olivaceous, or black in color; second through fourth abdominal segments with short, paired dorsolateral bars inclined cephalolaterally from cephalic margin, imparting in dorsal aspect "interrupted chevron" pattern; pleura of second through fifth segments with dark oblique blotch extending caudoventrally from base; caudal rim of each abdominal segment with narrow, light brown, orangish, or red band. Caudal portion of proximal segment of lateral ramus of uropod with transverse light brown band; ventral surfaces of uropods and telson with fine dark speckling. Dorsal surface of palm of chela orangish tan, dorsal surfaces of fingers darker, all with small flecks and some irregular spots or mottling; tips of fingers with crimson or orange band, subtended proximally by somewhat broader black band; large tubercle on dorsal palm proximal to articulation of dactyl crimson;

ventral surface of cheliped oyster with black flecking, tubercles at base of dactyl crimson; lateral margin of propodus with thin iodine or black line; articular eminences of chela and carpus of cheliped pale orange; distolateral spine of merus crimson. Pereiopods base color, with somewhat darker, mottled bands; margins and articulations crimson. Annulus ventralis and postannular sclerite gunmetal blue, except outer surfaces of cephalolateral prominences and region of sinus in caudal wall white. Antennular and antennal flagellae greenish brown proximally, changing to reddish tan distally.

Type locality—North Carolina, Jones County, Trent River (Neuse River basin) at State Road (SR) 1129 near junction SR 1131, ca. 4.5 air mi (7.2 air km) NNE of Comfort (Phillips Crossroads USGS Quadrangle, UTM coordinates 3882150/275010).

On 5 October 1978, when the holotype and several paratypes were collected, the river was about 10 m wide between banks, the abnormally low water was clear and shallow, and there was little or no visible flow. Pitted limestone outcrops were abundant at the site, and the limestone substrate was covered with fine silt, organic debris, and pale yellowish flocculence. Most of the 16 specimens of *O. carolinensis* collected were found under rocks. They were darkly encrusted and a great deal of flocculence was clinging to their setae. No other crayfishes were found at this site, but other aquatic invertebrates observed included Hemiptera of the families Nepidae, Notonectidae, and Belostomatidae; two kinds of Odonata nymphs; at least two kinds of mussels, one of them large and very abundant; several kinds of gastropods; aquatic Coleoptera, including a species of dytiscid; several kinds of unidentified insect larvae; and abundant *Palaemonetes paludosus* (Gibbes). A number of *N. lewisi* also were collected or observed.

Disposition of types—The holotype, allotype, and morphotype are in the crustacean collections of the North Carolina State Museum of Natural Sciences (NCSM), Raleigh (catalogue numbers NCSM C-2462, C-2486, and C-2463, respectively), as are the following paratypes: 1 ♂ II, 3 j ♂, and 2 j ♀ (NCSM C-78); paratypes consisting of 8 ♂ I and 1 ovig ♀ are in the United States National Museum of Natural History (USNM), Smithsonian Institution, Washington (USNM 332038).

Range and specimens examined—Endemic to the Neuse and Tar-Pamlico river basins of North Carolina. Within the Neuse basin, *O. carolinensis* occurs from near Willow Springs in southern Wake County, southeast to the upper reaches of the Trent River in central Jones County to Swift Creek on the line between Pitt and Craven counties. It appears to be absent from some of the Coastal Plain and most of the Piedmont Plateau of the Neuse River basin. Within the Tar-Pamlico

basin, the species occurs from headwater streams in the Piedmont of Granville County, east to western Halifax County and southeast to Pitt County. Specimens have been collected at the following localities (nearly all specimens are catalogued in the collections at NCSM, some are at USNM):

TAR-PAMLICO RIVER BASIN. *Edgecombe Co.*—(1) Tar R at US 64 bridge in Tarboro; 2 ♀, 19 Jan 1980, R. W. Mays; (2) Tar R at NC 42 E of Old Sparta, 5 air mi (8 air km) E center Pinetops; 4 ♂ I, 13 ♀, 30 Oct 1984, A. L. Braswell, JEC; (3) Tar R at Tarboro; 1 j ♂, 2 j ♀, ? Aug 1983, D. R. Lenat; (4) Tar R at NC 44 bridge, 1.6 air mi (2.6 air km) NNW Tarboro; 1 ♂ II, 5 ♀, 18 May 1986, ALB, D. Smith. *Franklin Co.*—(5) Shocco Crk at NC 58, 1.6 air mi (2.6 air km) N Centerville; 1 ♂ I, 17 Jan 1980, E. Rawls. *Franklin-Vance Co. line*—(6) Tar R at US 1; 1 ♂ II, 24 Jul 1993, D. G. Cooper, D. Jackan. *Granville Co.*—(7) Tar R at SR 1141, 0.9 air mi (1.4 air km) SSW Berea; 1 ♂ I, 1 ♂ II (molted to ♂ I), 6 ovig ♀, 1 ♀ & 1st-instar young, 6 May 1981, ALB; 1 ♂ II, 1 ♀, 17 Jun 1980, ALB, J. Cannon; 1 ♂ II, 1 ♀, 1 ♀ with exuvium, 4 Jun 1994, ALB, JEC; (8) Tar R ca. 0.5 mi (0.8 km) above SR 1133 bridge, ca. 1.8 air mi (2.9 air km) SE Providence; 2 ♀, 18 Aug 1980, ALB, J. H. Reynolds, C. Carnes; (9) Tar R at SR 1622, ca. 5.1 air mi (8.2 air km) SSW Dickerson; 1 ♂ I, 25 Feb 1980, ER; 1 ♂ I, 28 Jan 1980, ER; (10) Tar R at SR 1138, ca. 2.3 air mi (3.7 air km) N Culbreth; 1 ♂ I, 14 Nov 1981, R. E. Ashton, Jr., DS, P. Kumyhr; (11) Tar R at NC 96, 3.7 air mi (5.9 air km) NNW Wilton; 8 ♂ I, 1 ovig ♀, 16 Apr 1977, R. Thoma; 2 ♂ II, 1 ♀ with young, 18 May 1986, ALB, DS, D. Etnier. *Halifax Co.*—(12) Little Fishing Crk, ca 0.3 mi (0.5 km) below SR 1322 bridge, ca 2.7 air mi (4.3 air km) E Hollister; 4 ♂ I, 8 ♂ II, 12 ♀, 6 Aug 1980, ALB; (13) Bear Swamp at SR 1300, 6.7 air mi (10.7 air km) NNE Hollister; 1 ♂ I, 28 Feb 1980, RWM. *Nash Co.*—(14) Swift Crk at SR 1003, 3.3 mi (5.3 km) NE center Red Oak; 1 ♂ II, 8 Mar 1980, RWM; (15) Stony Crk at SR 1603, S jct SR 1609, 3.5 mi (5.6 km) S Red Oak; 1 ♂ I, 8 Mar 1980, RWM; (16) Tar R at SR 1746, 5 mi (8 km) SW Rocky Mount; 1 ♂ I, 25 Jan 1980, RWM. *Pitt Co.*—(17) Tar R at SR 1560, 1.3 air mi (2.1 air km) SE Pactolus; 1 ♀, 24 Mar 1980, JHR; (18) Tar R ca. 4 air mi (6.4 air km) E jct US 264 Bypass, 2 air mi (3.2 air km) NNE Simpson; 1 ♂ I, 29 Feb 1980, JHR; (19) Tar R ca. 2 air mi (3.2 air km) E jct SR 1565, ca. 2.8 air mi (4.5 air km) ENE center Grimesland; 1 ♀, 29 Feb 1980, JHR. *Warren Co.*—(20) Little Fishing Crk at SR 1532, ca. 3 air mi (4.8 air km) NNE Grove Hill; 2 ♂ I, 24 Mar 1980, ER; 2 ♂ I, 21 Mar 1980,

ER; (21) Reedy Pond Crk at SR 1510, ca. 1.6 air mi (2.6 air km) NNE Grove Hill; 2 ♂ I, 1 ♀, 19 Mar 1980, ER; 2 ♂ I, 17 Mar 1980, ER; (22) Shocco Crk at SR 1613, ca. 2.7 air mi (4.3 air km) NW Lickskillet; 3 ♂ I, 1 ♀, 10 Mar 1980, ER; (23) Fishing Crk at SR 1640, ca. 4.3 air mi (6.9 air km) SE Inez; 1 ♂ I, 14 Mar 1980, ER; (24) Fishing Crk at SR 1600, 2.9 mi (4.6 km) SSE Warrenton; 1 ♂ I, 27 Mar 1980, ER; (25) Shocco Crk at SR 1133, ca. 2.3 air mi (3.7 air km) SSE Vicksboro; 1 ♂ I, 14 Mar 1980, ER; (26) Fishing Crk at SR 1609, 4.4 mi (7.0 km) SSE Warrenton; 1 ♀, 26 Mar 1980, ER; (27) Possumquarter Crk at SR 1606, 3.5 mi (5.6 km) SSE Warrenton; 1 ♀, 17 Mar 1980, ER.

NEUSE RIVER BASIN. *Craven-Pitt Co. line.*—(28) Swift Crk at SR 1465 (Craven Co.), ca. 7.3 air mi (11.7 air km) W Vanceboro; 2 ♂ I, 19 Mar 1979, JHR. *Greene-Lenoir Co. line.*—(29) Contentnea Crk at SR 1004 (Greene Co.), 5.1 mi (8.2 km) SSE Hookerton; 1 ♂ I, 20 Mar 1979, P. S. Freed, E. Flowers. *Greene-Pitt Co. line.*—(30) Little Contentnea Crk at SR 1311, 2.5 mi (4.0 km) NNE Walstonburg; 2 ♂ I, 1 ♀, 9 Mar 1979, PSF. *Johnston Co.*—(31) Middle Crk at SR 1507, ca. 3.2 air mi (4.1 air km) ENE Willow Springs; 1 ♂ I, 1 ♂ II, 4 Apr 1979, A. P. Capparella; 1 ♂ I, 1 ♀ with young, 8 Apr 1979, APC; (32) Middle Crk at NC 210, ca. 3.2 air mi (5.1 air km) W Smithfield; 1 ♂ II, 3 j ♂, 2 j ♀, 28 Jul 1976, D. S. Lee, R. Franz; 16 j ♂, 4 ♀, 16 j ♀, 2 Aug 1976, DSL, M. M. Browne, Z. Sykes, MRC; (33) Middle Crk at SR 1504, 6.8 air mi (10.9 air km) W. Smithfield; 2 j ♂, 1 ♀, 2 Aug 1976, DSL, MMB, ZS, MRC; (34) Neuse R at SR 1201, 6.7 mi (10.7 km) SSW Princeton; 1 ♂ I, 18 Mar 1979, PSF. *Jones Co.*—(35) Beaver Crk at SR 1316, 6.2 air mi (9.9 air km) NW Trenton; 1 ♂ I, 6 Feb 1979, JHR; (36) Trent R at SR 1129, 4.5 air mi (7.2 air km) NNE Comfort (TYPE LOCALITY); 9 ♂ I, 7 ♀, 5 Oct 1978, ALB, REA, Jr., JEC; (37) Trent R at SR 1300, 4.8 air mi (7.7 air km) NW center Trenton; 9 ♂ I, 1 j ♂, 6 ♀, 1 j ♀, 1 Oct 1983, B. M. Burr, P. A. Burr; (38) Big Chinquapin Br at SR 1129, 0.8 air mi (1.3 air km) NE Phillips Crossroads; 1 ♂ I, 6 Feb 1979, JHR; (39) Beaver Crk at SR 1303, 5 air mi (8 air km) S Wyse Fork; 1 ♂ I, 14 Feb 1979, JHR; (40) Trent R at NC 58, 1.8 air mi (2.9 air km) ESE Phillips Crossroads; 1 ♂ I, 3 Sep 1985; DRL; (41) Trent R, 2.5 air mi (4.0 air km) WNW Pollocksville at Marine Corps Facility Oak Grove; 1 ♂ I, 22 Feb 1993; ALB, J. C. Beane. *Wake Co.*—(42) Middle Crk at SR 2739, 3.6 air mi (5.8 air km) E Willow Springs; 1 ♂ I, 13 Mar 1979, APC. *Wilson Co.*—(43) Turkey Crk just S Nash Co line, 1.0 air mi (1.6 air km) W Conner; number & sexes not available, 10 Jul 1985, V. Schneider.

Variations and anomalies—Individual variation in a number of characters is common, but no consistent hydrologic or geographic patterns are evident. Significant meristic and proportional variations are addressed in the "Diagnosis," but others also require notation. The distomedian eminence on the ventral surface of the carpus of the cheliped varies in development from a broad, rounded tubercle (rarely) to the usual prominent, acute spine that often is as long as the lateral and mesial spines of the podomere. Most individuals have a single cervical spine on each side of the carapace, but in 8.9 percent of 123 specimens there are 2 spines per side, and some animals have a single spine on one side and 2 on the other. One form I male has a tubercle and 2 spines on the left, 3 spines on the right. In some individuals, one or another of the cervical spines is bifurcate, and one female has two bifurcate spines on each side. In the same female, the right eye was yellow in life, and there are 3 spines instead of the normal 2 in each caudolateral corner of the cephalic section of the telson. There is also variation in the latter character in other specimens, but only one other individual, a form I male, has 3 spines in each corner. Small hepatic spines or spiniform tubercles are present in 6 of 123 specimens. One form I male shows a congenital lack of marginal spines on the rostrum, and in the same animal the mesial process of the left gonopod has a very acute tip with a minute notch in its caudal surface. Another form I male has a full-sized but deformed antennal scale projecting at nearly 90 degrees dorsally from the base of the normal left antennal scale. One female has a copulatory hook on the ischium of one of the third pereopods.

The fingers of the chela of females and form II males are essentially contiguous throughout their lengths when closed, but in form I males the fingers gape in the proximal half, and the proximal one-third of the opposable margin of the dactyl is moderately excised. In dorsal aspect, the central one-third of the dactyl in form I males is gently concave, then strongly recurved. In females, a single row of denticles extends distally along the opposable margin of the dactyl to the base of the cornified tip. In form II males there are one or two such rows of denticles, and in form I males there are three or four rows. The antennae of form I males are slightly longer than those of form II males and females.

Size—The largest specimen in our samples is a form I male of 34.1 mm TCL (23.6 mm PCL). Only eight other adult males have TCLs in excess of 30 mm. The smallest form I male measures 15.8 mm TCL (10.8 mm PCL). Fourteen other form I males have TCLs of less than 20 mm, and the mean of 55 form I males is 24.6 mm.

Only two large form II males have been collected; one (the morphotype) is 23.9 mm TCL (17.1 mm PCL), and the other is 24.3 mm TCL (16.7 mm PCL). The largest female measures 32.8 mm TCL (24.1 mm PCL). Five other females have TCLs greater than 28 mm. The smallest female with attached ova or young measures 17.1 mm TCL (11.3 mm PCL), and the largest female in this condition measures 25.3 mm TCL (18.1 mm PCL). Assuming 17.1 mm as the lower limit of TCL for sexually mature females (range = 17.1–32.8 mm; $n = 46$), the mean TCL for this group is 23.4 mm. The TCLs of 101 form I males and mature females range from 15.8 to 34.1 mm (both extremes are males) and the mean is 24.1 mm.

Life history notes—Form I males have been collected in every month except June, July, and December, but were preponderant in the spring and fall. Of 71 such males, 22 were collected in March, 10 in April, and 22 in October. A form II male collected on 6 May 1981 molted to form I on 3 July 1981 in the laboratory.

Females bearing ova or young have been collected only in April and May. An unmeasured female taken on 8 April 1979 had two third-instar young attached, and a female measuring 18.7 mm TCL (13.4 mm PCL), collected on 16 April 1977, was carrying 39 ova of about 1.8 mm diameter. The latest date on which a female carrying young has been found was 18 May 1986. Table 2 provides data for six laden females collected at the same site on 6 May 1981.

Crayfish associates—Cooper and Ashton (1985) and Cooper and Braswell (1995) briefly discussed the decapod fauna of the Neuse and Tar-Pamlico basins. The crayfish associates encountered with greatest frequency in *O. carolinensis* samples were *Cambarus* (*Depressicambarus*) *latimanus* (LeConte) and *Cambarus* (*Puncticambarus*) *acuminatus* Faxon (s.l.). *Procambarus* (*Ortmannicus*) *acutus* (Girard) was the third most often collected species in these samples, and all three of these associates appeared together in some of them. *Cambarus* (*Lacunicambarus*) *diogenes* Girard also was included in several of the collections. Generally, *C. acuminatus* (s.l.) and *C. latimanus* far outnumbered *O. carolinensis* in samples where they were taken together. At a few localities, however, *O. carolinensis* either outnumbered any other species found, or was the only species collected. Although *Fallicambarus* (*Creaserinus*) *fodiens* (Cottle), *Cambarus* (*Depressicambarus*) *reduncus* Hobbs, and *P. medialis* have been found in open water in both river basins, they have not been taken at any *O. carolinensis* site.

Relationships—The general features of the form I male gonopod (terminal elements long and of subequal length, subparallel, subsetiform) and the female annulus (well defined sulcus, deep fossa, large and

Table 2. Data for six laden female *Orconectes (P.) carolinensis*, new species, collected at the same site on 6 May 1981.

TCL (PCL)	Condition
17.1 (11.5)	28 ova (1.8-1.9 mm diam)
19.5 (13.7)	59 ova (1.7-1.9 mm diam), 3 of them beginning eclosion, and several empty egg cases
20.4 (14.3)	76 ova (1.7-1.8 mm diam)
21.2 (14.9)	29 first-instar young and 1 unhatched ovum
23.8 (16.7)	16 first-instar young and 60 ova (1.9-2.0 mm diam) undergoing eclosion
25.3 (18.0)	109 first-instar young and 2 unhatched ova

lobiform cephalolateral prominences overhanging fossa and separated by deep trough) are typical of subgenus *Procericambarus* (Fitzpatrick 1987:57–58). However, the upper limit of the range for length of the terminal elements of the mature gonopod, expressed as percent of total length of the appendage, is slightly higher for *O. carolinensis* (range = 46.5–57.9% \bar{x} = 51.6%, n = 54) than for the subgenus (range = 34–55%). In addition, the range for areola length, expressed as percent of TCL, is considerably lower for *O. carolinensis* (range = 25.5–31.1%, \bar{x} = 28.5%, n = 113) than for the subgenus (range = 29–37%). Within *Procericambarus*, *O. carolinensis* clearly has its greatest affinities with several members of the Spinosus Group, as defined by Fitzpatrick (1987:58). Its closest relatives almost certainly are *Orconectes (Procericambarus) spinosus* (Bundy), of the Tennessee and Coosa river basins, and *Orconectes (Procericambarus) putnami* (Faxon), which occurs in parts of the Ohio River drainage.

The new species may be distinguished from its relatives in the Spinosus Group by the following: (1) the greater length of the terminal elements of the mature gonopod (range for the Spinosus Group is 40-48% of total gonopod length); (2) the shorter, broader areola, and the greater number of punctations across the narrowest part; (3) the somewhat longer acumen and rostrum, the latter being deeply excavate, much more punctate and setiferous, and with thicker margins; (4) the smaller size (see section on "Size" for data); (5) the lack of a clearly defined ventral row of tubercles subtending the row on the mesial margin of the palm; (6) fewer tubercles in the ventralmost and dorsalmost rows of the mesial margin of the dactyl; (7) the far greater number of spiniform tubercles on the ventrolateral ridge of the merus, these being generally strong, acute spines, especially in the distal half to

two-thirds of the podomere, as opposed to small (often minute) tubercles; (8) fewer but much more highly developed tubercles on the ventromesial ridge of the merus; (9) the presence of 3 or more, usually spiniform and sometimes bifurcate, tubercles on the ventromesial ridge of the ischium; and (10) the occasional presence of multiple cervical spines (and small, spiniform hepatic tubercles).

A few of the characters exhibited by *O. carolinensis* could be interpreted as plesiomorphies within the subgenus. These include multiple cervical spines and spiniform hepatic tubercles in some specimens, a generally more spinose mien, a short, broad areola, and a color pattern that includes a "saddle" on the carapace. It is tempting to conclude that it is one of the phylogenetically older species within the *Spinosus* Group and perhaps within the subgenus. On the other hand, the various spines and spiniform tubercles could also represent periodic recurrences of atavisms. Until such time as the other members of the *Spinosus* Group, especially *O. spinosus* and *O. putnami*, have been described and defined more thoroughly, any conclusions as to the relative "age" of *O. carolinensis* would be premature.

Remarks—Fitzpatrick (1987:69) hypothesized that the progenitors of *Procericambarus* occupied the southern extremities of the eastern part of the Tennessee River, and that their establishment there "may have taken place in early Quaternary times." From this center they spread over the Cumberland Plateau, entered the Ohio system, and expanded west. Today the subgenus occupies a broad range that extends from the Blue Ridge into eastern Oklahoma and Kansas, and the disjunct *O. carolinensis* is the only representative inhabiting Atlantic Coast drainages. In North Carolina, the easternmost montane populations of the *Spinosus* Group occur in the New and upper Little Tennessee river basins (Cooper and Braswell 1995), from approximately 270 to 480 air km (170 to 300 air mi), respectively, west of the westernmost populations of *O. carolinensis*. It seems reasonable, considering the incontrovertible affinities of the species, that it derived from an ancestor that was part of an early and aggressive *Procericambarus* stock that was widespread in the pre-glacial Teays River and the upper reaches of the Tennessee River. If true, this upland stock could only have gained access to the Atlantic versant by means of a breach of the Blue Ridge and subsequent capture of some upper Teays headwaters by an east-flowing Piedmont stream. Ross (1969:283–290) persuasively argued that, in the area under consideration, this probably was accomplished "in early Pleistocene time" by headwaters of the young Roanoke River. Subsequent southeastward dispersal of this putative ancestor in the Greater Roanoke system would have brought it into waters

contiguous or interdigitating with those of the adjacent Greater Pamlico River, later (probably late in the Pleistocene) to become the separate but twin systems now known as the Neuse and Tar-Pamlico rivers. Jenkins et al. (1971:45) indicated the presence of a theater of stream capture between the Roanoke and what are the headwaters of today's Tar and Neuse rivers, which we interpret to have been in the area of present Person and Granville counties. It is reasonably parsimonious to conclude that it was through such piracies, from Teays to Greater Roanoke to Greater Pamlico, that the ancestor of *O. carolinensis* gained access to and became isolated in the latter system, there to evolve allopatrically into the present species. This dispersal, particularly between the contiguous Roanoke and Neuse-Tar systems where downslope differences in elevation occurred and drainage divides were not of excessive magnitude, could have been abetted by the flooding that likely would have been prodigious during interglacial periods, and perhaps even by relatively minor tectonic events.

Jenkins et al. (1971:82) postulated a generally similar dispersal history for the ancestor of *N. furiosus*. On the other hand, Sessions and Wiley (1985), on the basis of their karyological studies and electrophoretic analyses provided by Ashton et al. (1980), considered *Necturus lewisi* to be the most primitive of the extant species of the genus *Necturus*, and the widespread western *N. maculosus* to be the most derived. They suggested that the *Necturus* stock initially spread south in the Atlantic Coastal Plain, then west through the Gulf regions and around the southern Appalachians, and finally north in the Ohio and Mississippi drainages.

As earlier mentioned, *O. carolinensis* occupies the entire Tar-Pamlico watershed, but appears to be absent from some parts of the Neuse watershed, including nearly all of its Piedmont streams. If not a sampling deficiency, this could indicate that the initial entry of its ancestor into the Greater Pamlico River occurred in an extensive northernmost (Tar River) portion, and expansion of the species in the current Neuse basin is an ongoing process. If so, this stream dweller likely will never extend its range upriver into the Eno, Little, and Flat rivers, since the Neuse River has been impounded to create Falls Lake, which stretches for about 35 km (22 mi) from northwestern Wake County into Granville and Durham counties, and has converted most of the Neuse and its tributaries in those areas to lacustrine habitats.

Etymology—*Carolinensis*, after North Carolina, to which the new species is endemic. Suggested vernacular name: North Carolina Spiny Crayfish.

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Nine-banded Armadillo, *Dasypus novemcinctus*
(Mammalia: Edentata), in South Carolina: Additional
Records and Reevaluation of Status

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ABSTRACT—The nine-banded armadillo (*Dasypus novemcinctus* Linnaeus) has been undergoing range expansion and is now established throughout much of the southeastern United States. Previous records for South Carolina are widely scattered, and no evidence of an established population has been reported. We present an additional museum record, not previously reported, and field observations of living and road-killed animals that strongly suggest a population of armadillos is established in southwestern South Carolina. This range extension into South Carolina probably occurred within the past ten years. Henceforth, the nine-banded armadillo should be considered an established member of South Carolina's mammalian fauna.

The nine-banded armadillo has been undergoing a natural expansion into the southeastern United States over the past 100 years. This expansion began when animals moved into Texas from northern Mexico in the mid-1800's, perhaps in response to changing land use practices. By 1954 armadillos had reached the Mississippi River, and by 1972 were in the western Florida panhandle. Armadillos were also introduced into peninsular Florida between 1920 and 1936, and the two subpopulations merged in the mid-1970's (Talmage and Buchanan 1954, Humphrey 1974). This species is now established in eight states (Texas, Oklahoma, Arkansas, Louisiana, Mississippi, Alabama, Florida, and Georgia), and is expected to continue to move northward and eastward until limited by low winter temperatures (Humphrey 1974).

The distribution and status of the nine-banded armadillo in South Carolina is problematical. Webster et. al. (1985) stated that South Carolina might represent the northernmost limit of the armadillo's expanding range, but concluded its status was uncertain. Hall's (1981) range map included most of South Carolina based on three records from Golley (1966), which the latter believed to be translocated animals. Humphrey (1974) listed a single occurrence based on a widely circulated questionnaire, and Sanders (1978) reported ten records from scattered Coastal Plain and Piedmont locations. More recently Mayer (1989) summarized all previous state records, reported two additional animals, and 15 recent sightings listed by respondents to a questionnaire (Mayer 1989). Given the proximity of many previous records to major highways, some believe these reports represent escaped or released animals rather than pioneering individuals at the forefront of an expanding range (Golley 1966, Sanders 1978, Mayer 1989). Mayer (1989) concluded that because direct evidence of an established population is lacking, the status of the species in South Carolina remains uncertain.

METHODS

We present an additional museum record, not previously reported, and field observations from southwestern South Carolina. The museum specimen (Clemson University Vertebrate Collection #126) was collected 9 December 1978 on Port Lamar Road, Cessionville, Charleston County. Field observations were made in Jasper, Allendale, and Barnwell counties during April, May, August, and October 1995 (Table 1). Specific locality data for all records were deposited in the files of the Clemson University Vertebrate Collection (CUSC).

RESULTS AND DISCUSSION

Four road-killed and two living animals were found in five nights (ca. 9.5 hours) of collecting along a 17.6-km segment of Sandhills Road (County Road 119), due west of Tillman. Furthermore, numerous tracks and probe-holes made by foraging armadillos (Murie 1954) were noted at the Tillman Sand Ridge Natural Heritage Preserve on Sandhills Road. This road is a popular collecting location for reptile enthusiasts, and others also report frequent sightings of road-killed and living armadillos here (Todd Kuntz, United States Forest Service, personal communication). Another road-killed armadillo was found in Jasper County on Cohen Road (County Road 22), ca. 10 km northeast of Tillman. Two additional road-killed animals were also found in Barnwell and Allendale counties. We are unaware of any other reports of such a temporal and spatial

Table 1. Summary of recent nine-banded armadillo (*Dasypus novemcinctus*) records from southwestern South Carolina.

Date	Condition ¹	Sex	Location	Remarks
29 April 1995	DOR	F	Sandhills Rd., Jasper Co.	Badly damaged, not collected
15 May 1995	AOR	?	Sandhills Rd., Jasper Co.	
15 May 1995	AOR	?	Sandhills Rd., Jasper Co.	
16 May 1995	DOR	?	Sandhills Rd., Jasper Co.	Decomposing, not collected
25 August 1995	DOR	M	Sandhills Rd., Jasper Co.	Skull collected (CUSC # 838)
25 August 1995	DOR	?	Sandhills Rd., Jasper Co.	Remains of carapace only
2 October 1995	DOR	?	SC Hwy 39, Barnwell Co.	Dried remains, not collected
7 October 1995	DOR	?	Cohen Rd., Jasper Co.	Badly damaged, not collected
7 October 1995	DOR	?	Sanddoz Rd., Allendale Co.	Decomposing, partially eaten by vultures

¹ DOR—Dead on road; AOR—Alive on road.

concentration of records within this state. We believe these records strongly suggest that the nine-banded armadillo is now established in extreme southwestern South Carolina.

The timing of this range extension into South Carolina remains speculative, but probably occurred within the past ten years. Humphrey (1974) places the northernmost range limit in the Coastal Plain near McIntosh County, Georgia, approximately 80 km south of the Savannah River. In the absence of physical or climatic barriers, an average invasion rate of four to 10 km per year has been estimated (Humphrey 1974). This model predicts an extension into South Carolina by the early to mid-1980's. The Savannah River could have slowed immigration, but armadillos are known to cross major rivers by swimming or bottom walking (Talmage and Buchanan 1954). Wright (1982) did not find armadillos among mammals using gopher tortoise (*Gopherus polyphemus*) burrows on Tillman Sand Ridge Natural Heritage Preserve, although they are reported to inhabit tortoise burrows elsewhere (Jackson and Milstrey 1989). Thus, we speculate armadillos did not become established in Jasper County until 1985 or later. This coincides with the 1985 and 1986 records reported by Mayer (1989) further north in Aiken and Barnwell counties. Invasion is especially rapid in river valleys, and the Savannah River may be functioning as a dispersal corridor. Range expansion is expected throughout South Carolina, with the exception of the mountainous northwestern corner of the state where low temperatures likely preclude overwinter survival (Humphrey 1974, Mayer 1989).

CONCLUSIONS

It appears that numbers of armadillos are present in at least one area of southwestern South Carolina. Further range expansion can be expected in the state, particularly throughout the Savannah River drainage and Coastal Plain. Henceforth the nine-banded armadillo should be considered an established member of South Carolina's mammalian fauna.

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Post-hibernation Movement and Foraging Habitat of a Male Indiana Bat, *Myotis sodalis* (Chiroptera: Vespertilionidae), in Western Virginia

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ABSTRACT—We investigated departure patterns of bats from a hibernaculum and use of tree roosts and foraging habitat by a male Indiana bat (*Myotis sodalis*) in western Virginia with radio-telemetric techniques, cave population surveys, and habitat assessment. Although hibernating Indiana bats are well documented in Virginia, our study is the first to report foraging and roosting habitat in Virginia, which is along the eastern periphery of the range of the species. After departure from the hibernaculum in late April, a radio-tagged male *M. sodalis* moved 16 km southwest where it remained for two weeks until the radio transmitter failed. This bat used a mature, live, shagbark hickory (*Carya ovata*) tree as a diurnal roost; up to 10 other bats roosted in the same tree. The bat primarily foraged among tree canopies within 625-ha area of an 80-year-old, oak-hickory forest. Our study suggests that male *M. sodalis* use foraging areas and tree roosts found in the area of hibernacula. Thus, we recommend that conservation efforts protect and manage foraging and tree roosting habitat in the vicinity of *M. sodalis* hibernacula.

Approximately 85% of all Indiana bats (*Myotis sodalis* Miller and Allen) hibernate in seven caves located in Missouri, Indiana, and Kentucky (Harvey 1992). Indiana bats are most common in the Midwest, with peripheral populations in northeastern (e.g., Pennsylvania), Atlantic (e.g., Virginia), southeastern (e.g., Georgia), and northern midwestern (e.g., Michigan) states (Humphrey 1978). Peripheral populations may become increasingly important in the management of this federally

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endangered species if larger populations continue to decline. Populations of *M. sodalis* hibernating in Virginia caves typify a peripheral population, as they occur on the eastern edge of the range and represent <1% of the total estimated population (Dalton 1987). Ten known *M. sodalis* hibernacula occur in Virginia accounting for 2,500 individuals.

Knowledge of summer foraging areas and roost sites of *M. sodalis* is as important to conservation efforts as identification and protection of hibernacula, but the former remain poorly documented (Humphrey et al. 1977, Thomson 1982). Most information on summer foraging and roosting habitat of *M. sodalis* comes from the central area of the range of the species (i.e., midwestern United States), with an emphasis on maternity sites. In Illinois and Indiana, female *M. sodalis* roost in several species of trees including shagbark hickory (*Carya ovata*), bitternut hickory (*C. cordiformis*), green ash (*Fraxinus pennsylvanica*), eastern cottonwood (*Populus deltoides*), northern red oak (*Quercus rubra*), post oak (*Q. stellata*), shingle oak (*Q. imbricaria*), and sycamore (*Platanus occidentalis*) (Humphrey et al. 1977, Gardner et al. 1990, Kurta et al. 1993). In addition, Humphrey et al. (1977) identified a maternity roost under loose bark of a dead bitternut hickory tree. Females and newly volant young *M. sodalis* forage in riparian habitat, along the edge of floodplain forest and within forest canopies (Humphrey et al. 1977, Laval et al. 1977); however, roosting and foraging habitats of male *M. sodalis* are less well known. Observations in Missouri indicate that males forage along ridges and hillsides around forest canopies (Laval et al. 1977).

Migratory behavior may differ among male and female *M. sodalis* (Hall 1962). Females migrate from hibernacula to maternity sites, whereas males either move away from or remain near the hibernacula during spring and summer. This suggests that suitable foraging and roosting habitat for *M. sodalis* occurs in the vicinity of some hibernacula. Although the distribution and abundance of *M. sodalis* hibernating in Virginia caves has been well documented, no summer roost sites, maternity colonies, or summer foraging habitats have been identified in the state prior to our study. Our objectives were to determine if male *M. sodalis* wintering in a Virginia cave remained in the vicinity of the hibernaculum during spring and summer months, and to characterize foraging and roosting habitats of male *M. sodalis*.

METHODS

We studied a *M. sodalis* colony that hibernates in a cave in Bath County, Virginia. Bath County is located in a rural area of the Appalachian Mountains in western Virginia within the George Washing-

ton National Forest. An active timber management program is practiced in this forest. We monitored emergence and departure patterns at the cave entrance between March and early May 1993. Using night-vision goggles, emergence patterns at the cave entrance were monitored by observing the numbers of individuals entering and leaving the cave. Mist nets (one net covering cave entrance) and harp traps were used to census species emerging from the cave (7 net nights, from sunset to approximately 0100 hours; one net night = 1 open net per night). We used head lamps with red filters and infrared goggles to aid in estimating numbers of individuals for all species in the cave. *Myotis lucifugus*, *M. septentrionalis*, *M. leibii*, *Eptesicus fuscus*, *Pipistrellus subflavus*, and *M. sodalis* were known to hibernate in the cave. The abundance of *M. sodalis* in the cave was determined five times (3, 17, 24, 28 April, and 1 May) to establish spring departure patterns for this species.

On 28 April 1993, two male *M. sodalis* were captured in the cave and fitted with 0.65-g radio transmitters (Holohill Systems, Ltd., 3387 Stonecrest Road, Woodlawn, Ontario, Canada). Transmitters were equivalent to 6% of the body mass of each bat. Transmitters were attached between the shoulder blades with eyelash glue (no hair was removed). Each bat was placed in a cloth sack for approximately 30 minutes to allow the glue to dry before they were released. The bats were released 15 minutes apart approximately 200 m south of the cave entrance, and tracked with radio receivers (Wildlife Materials, Model TRX2000S, Route 1 Box 427A, Carbondale, Illinois 62901) for the life of the transmitter batteries. Triangulation techniques using two or three observers, direct observation, and the receiver's attenuator were used to identify the roost site, to delineate foraging areas, and to identify movement patterns.

Vegetative characteristics of foraging and roosting habitats were assessed with the point-quarter sampling technique (Brower et al. 1989) and visual observation. Points of vegetative sampling occurred along seven 100-m transects. For each transect, five points were determined, and four trees were sampled at each point for a total of 140 trees sampled for all seven transects. Additional data were collected at the tree roost using mist nets (2 net nights; see Gardner et al. 1989 for description of mist netting system) and infrared goggles, the latter to determine activity patterns (time of emergence from roost) and numbers of bats associated with the tree roost. The tree roost was not mist netted due to its height above ground and the steep slope of the terrain. Forest habitat, streams, and roads surrounding foraging and roosting habitats were sampled with mist nets (11 net nights).

RESULTS AND DISCUSSION

In winter 1992, 38 *M. sodalis* and 1,686 bats were hibernating in the cave (Leffler et al. 1993). Few individuals left the cave in early April, with most bats departing by early May. Trapping at the cave entrance resulted in 56 captures (all adults), including 19 *Myotis lucifugus*, 17 *M. septentrionalis*, 5 *M. leibii*, 4 *Eptesicus fuscus*, and 11 *Pipistrellus subflavus*. *M. sodalis* were not captured during this period. The 56 bats captured account for only 4% of the hibernating population of bats in the cave. Assuming that no *M. sodalis* had left the cave before our first census, the *M. sodalis* population in the cave declined from 31 to 18, 8, 6, and 0 individuals on 3, 17, 24, 28 April and 1 May, respectively. By mid-April the single cluster of *M. sodalis* had broken into several small clusters within a 2-m² area. Cope and Humphrey (1977) reported similar trends in departure patterns of *M. sodalis*, where females left the hibernaculum before males, and most bats departed by late April and early May.

Two radio-tagged male *M. sodalis* were tracked for approximately one hour after release near the cave, at which time signals of both individuals were lost. Bat #440 was never located from the ground after release, but its signal was detected by an aircraft in the cave area on 8 and 10 May. Bat #458 was relocated by ground in the George Washington National Forest on 1 May, approximately 16 km SW of the hibernaculum. Bat #458 roosted and foraged in George Washington National Forest until 20 May when the transmitter battery failed. For 19 nights, bat #458 roosted on a north facing slope (0° to 5° east of north) at 700 m elevation, beneath the bark of a mature shagbark hickory (ca. 30 m in height, 61 cm DBH). The bat roosted at a height >8 m in the shagbark hickory. Other tree species within a 10-m radius of the roost tree included basswood (*Tilia* spp.), red maple (*Acer rubrum*), eastern hophornbeam (*Ostrya virginiana*), tulip poplar (*Liriodendron tulipifera*), and pignut hickory (*Carya glabra*). Bat #458 was not the only bat using the shagbark hickory for a roost; on separate occasions at dusk 5, 10, and 3 bats emerged from the roost tree. Leaving the roost tree around 2030 hours nightly, bat #458 was one of the first bats to emerge, with the other bats emerging by 2100 hours. Bat #458 immediately left the area of the roost tree upon emergence and flew to foraging habitat, located within 1 km of the roost tree. Mist netting the roost site and foraging habitat resulted in capture of 2 *Lasionycteris noctivagans*, 3 *Lasiurus borealis*, 4 *Eptesicus fuscus*, 6 *Pipistrellus subflavus*, 6 *Myotis lucifugus*, and 3 *M. septentrionalis*; but, no *M. sodalis* were captured.

After emerging from the roost tree, bat #458 foraged persistently

throughout the night, often until after 0200 hours. On 2 of 19 nights, the bat ceased foraging for approximately one hour around 2300 hours. Foraging habitat for bat #458 encompassed approximately 625 ha. A small, two-lane road and an unimproved forest service road transected the habitat. A small first-order stream ran parallel to the two-lane road. Foraging habitat was an 80-year-old, mature oak-hickory mixed deciduous forest with a conifer component (Table 1). When foraging in the 625 ha habitat, this bat spent the majority of its time flying in an elliptical pattern at canopy height. The ellipse was transected by a small two-lane road, which was occasionally used as a flyway. Bat #458 was also observed flying in an elliptical pattern along a ridge containing a patch of mature hemlocks. On two occasions at dusk, the bat was observed foraging along a water course within 0.5 km of the roost site. In Missouri, Laval et al. (1977) found that male *M. sodalis* forage in elliptical patterns among treetops of dense forest along ridges and hillsides instead of over water. Humphrey et al. (1977) also reported *M. sodalis* foraging around tree canopies.

Table 1. Diameter at breast height (DBH), density, and relative frequency of tree species within the foraging area of a male *M. sodalis* in Bath County, Virginia. A total of 140 trees were sampled within the foraging habitat.

Tree Species	DBH (cm)		Density (Trees/ha)	Relative Frequency
	Mean (\pm SE)	Range		
<i>Acer rubrum</i>	13.3 \pm 2.0	33 - 8	66	0.091
<i>Carya glabra</i>	22.5 \pm 1.3	24 - 20	17	0.027
<i>C. ovata</i>	20.0 \pm 3.0	30 - 14	28	0.045
<i>C. tomentosa</i>	30.0 \pm 3.5	38 - 21	50	0.082
<i>Cornus florida</i>	11.8 \pm 1.0	17 - 9	50	0.064
<i>Fagus grandifolia</i>	17.3 \pm 4.3	38 - 10	33	0.045
<i>Juglans nigra</i>	19.5 \pm 3.3	27 - 10	28	0.027
<i>Liriodendron tulipifera</i>	37.8 \pm 8.8	84 - 9	50	0.082
<i>Pinus strobus</i>	23.5 \pm 2.5	46 - 9	89	0.091
<i>Quercus rubra</i>	40.0 \pm 3.8	72 - 9	94	0.127
<i>Q. alba</i>	36.8 \pm 4.0	52 - 24	39	0.055
<i>Tilia</i> spp. (unidentified)	23.0 \pm 2.5	32 - 14	39	0.064
<i>Tsuga canadensis</i>	28.3 \pm 3.8	64 - 8	111	0.136
other ¹	12.5 \pm 1.8	20 - 8	44	0.064

¹ Includes infrequent occurrence of *Acer pennsylvanicum*, *Betula lenta*, *Carpinus caroliniana*, and *Ulmus rubra*.

CONCLUSIONS

Although foraging habitat and roost site use by *M. sodalis* in Virginia are based on data from one bat, our study is consistent with studies conducted in other geographic regions. Because the male *M. sodalis* remained in the vicinity of the hibernaculum during spring, our study suggests that foraging areas and tree roosting habitats for male *M. sodalis* may be found near hibernacula. Conservation practices dictate that identification and protection of roosting and foraging habitat is necessary for bat conservation efforts.

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The Milliped Family Hirudisomatidae in the New World (Polyzoniida)

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Abstract—In the New World, the milliped family Hirudisomatidae is represented by *Octoglena* Wood, with five species, and the monotypic new genus, *Mexiconium*. *Octoglena bivirgata* Wood, *O. anura* (Cook), n. comb., and *O. prolata*, n. sp., are contiguous along the Pacific Coast from British Columbia to Santa Cruz County, California; *O. sierra*, n. sp., is a localized, allopatric species in the Sierra Nevada foothills; and *O. gracilipes* (Loomis), n. comb., occurs in the eastern United States from South Carolina to Tennessee and Alabama. *Mexiconium absidatum*, n. sp., the first record of the family from Mexico, occurs at a high elevation in the Sierra Madre Oriental, Vera Cruz. *Octoglena bivirgata* displays three dark dorsal stripes, and *M. absidatum* exhibits a dark, middorsal stripe; the other species are pale yellowish to white. The following new synonymies are proposed: *Hypozoneum* Cook and *Euzoneum* Chamberlin under *Octoglena*, and *H. arnaudi* and *E. crucis*, both by Chamberlin, under *O. bivirgata*. The Hirudisomatidae represents an Ancient Holarctic faunal assemblage that spread across North America from east to west, and southward into Mexico, and has experienced considerable extinction. *Octoglena* is one of five Nearctic genera exhibiting east/west disjunctions, and a secondary center of evolution exists along the Pacific Coast. Relationships within *Octoglena* are *gracilipes* + (*sierra* + (*anura* + (*prolata* + *bivirgata*))).

In the Western Hemisphere, the milliped order Polyzoniida is represented by the pantropical family Siphonotidae, with two genera in South America and the common synanthrope, *Rhinotus purpureus* (Pocock), in the West Indies, Florida, Louisiana, and Central America (Hoffman 1977, 1980), and the Holarctic families Polyzoniidae and Hirudisomatidae, in the eastern and western United States. The latter spreads northward into coastal British Columbia, and an allopatric species occurs in the Sierra Madre Oriental, Vera Cruz, Mexico (Fig. 1). The east-Nearctic polyzonoid fauna comprises six species of *Polyzoneum* Brandt (Polyzoniidae) (Loomis 1971; Shelley 1976, 1988) and one hirudisomatid that was erroneously placed in this genus and family. The western fauna of this order has never been examined and presently consists of seven genera and ten nominal species (Chamberlin 1954,

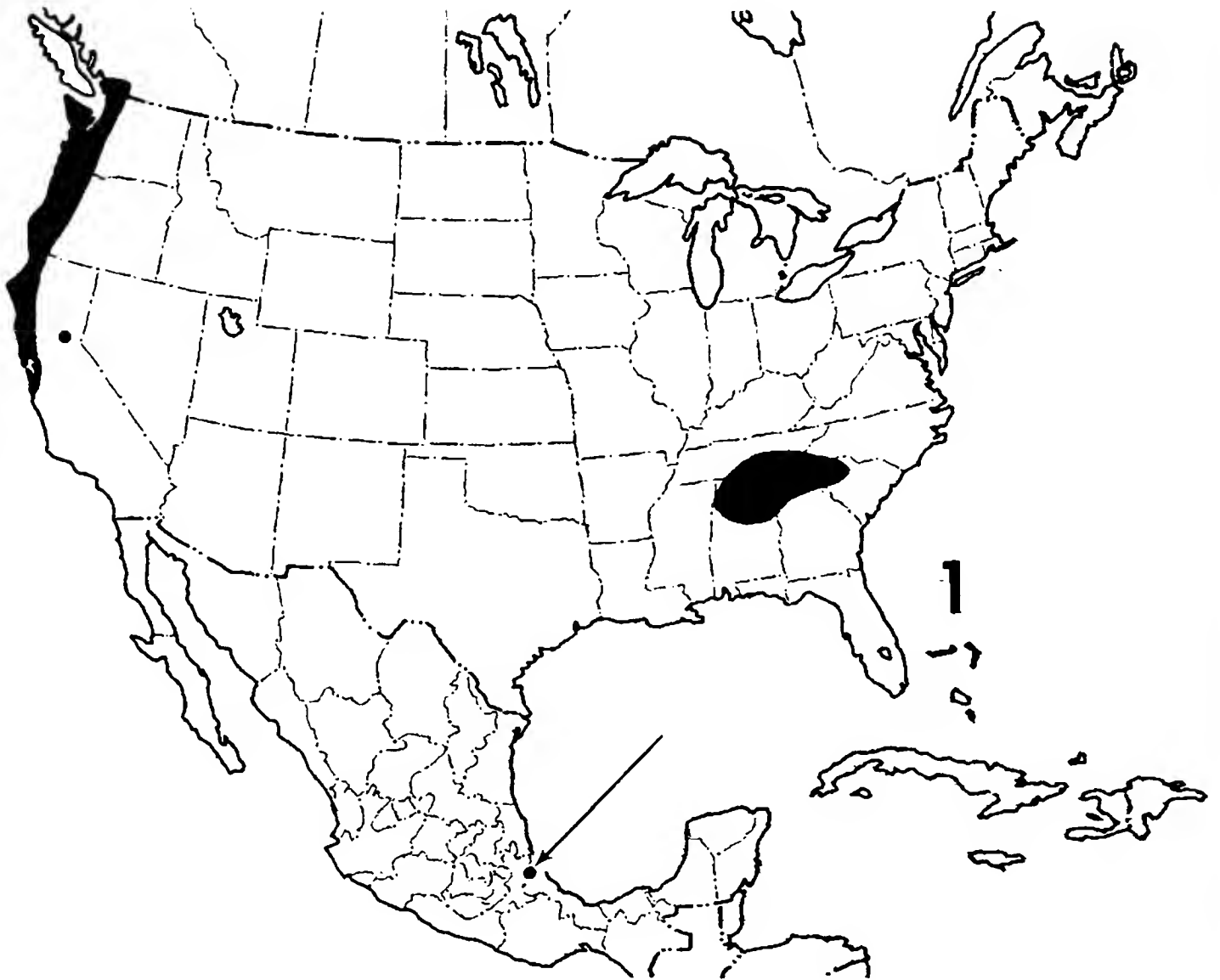


Fig. 1. Distribution of the Hirudisomatidae in the New World, showing the areas occupied by *Octoglena* in the eastern and western United States and British Columbia, and the single site of *Mexiconium*, denoted by the dot and arrow, in Mexico. The dot in California represents the two localities of *O. sierra*.

Chamberlin and Hoffman 1958). Hoffman (1980) and Shelley (1988) referred *Octoglena* and *O. bivirgata*, both authored by Wood, to the western fauna and the Hirudisomatidae, because its striped color pattern (Wood 1864, 1865) is displayed by two California hirudisomatids, *Euzonium crucis* and *Hypozoneum arnaudi*, both authored by Chamberlin, whereas no eastern polyzonioid is so marked. Studies are progressing on the west-Nearctic Polyzoniidae, so this contribution addresses the Hirudisomatidae and transfers the east-Nearctic representative into *Octoglena*; I also erect a new genus, *Mexiconium*, to accommodate the Mexican species. *Octoglena* is therefore a continental taxon and similar to *Brachygybe* Wood (Platydesmida: Andrognathidae), *Orinisobates* Lohmander (Julida: Nemasomatidae), *Scytonotus* Koch (Polydesmida: Polydesmidae), and *Ergodesmus* Chamberlin (Polydesmida: Nearctodesmidae) in exhibiting east/west disjunctions (Fig. 1) (Gardner 1975, Enghoff 1985, Shelley, 1993, 1994a). I do not address here the larger

question of the distinction(s) between the New World hirudisomatids and the European genus, *Hirudisoma* Fanzago, which requires comparative material of its eight species (keyed by Mauriès 1964), nor do I assess differences with *Orsiboe* Attems and *Kiusiozonium* Verhoeff in Japan, and the former may belong to another family (Hoffman 1980, personal communication).

Polyzonioid gonopods tend to be structurally conservative and lack the dramatic elaborations of polydesmoids that typically form the bases of generic diagnoses; consequently, genera are often distinguished by subjective somatic features. *Octoglena gracilipes* (Loomis), in the eastern United States, differs somatically from the western species in its narrower telson and the absence of a slight caudolateral extension to the midbody metatergites (Figs. 8, 12, 23-24). Its anterior gonopod differs from those of the Pacific Coastal species, but this anatomical gap is bridged by *O. sierra*, n. sp., in the Sierra Nevada, which occupies an intermediate geographical position. Separate generic status for *gracilipes* could be based on the somatic features, but I think these differences are insignificant when compared to the gonopodal linkage that unites *gracilipes* with the Pacific Coastal components; I therefore opt for a single genus, for which *Octoglena* is the oldest available name. Similarly, the anterior gonopod of the Mexican hirudisomatid resembles that of *O. sierra*, but its somatic differences are much greater and, in my view, require generic recognition. The metatergites do not extend laterad, and the body form is fundamentally different, the segments being narrower and more vaulted than the flattened, "bell shaped" segments of *Octoglena* (Figs. 7, 35). There is also one broad, middorsal stripe rather than three, as in *O. bivirgata* (Figs. 2, 31-33), and there are two pairs of ocelli rather than three (Figs. 6, 22, 34).

Hirudisomatids are not readily distinguished from polyzoniids, as most characters have exceptions. For example, the caudal metatergal margins of *O. bivirgata* are strongly upturned and clearly differentiate it from the flush condition in sympatric polyzoniids, but this feature is less distinctive for *O. anurum* and *O. gracilipes*, which can be confused with polyzoniids. The margins of *M. absidatum* are slightly elevated but not upturned, and hence resemble the closely appressed tergites of polyzoniids. West-Nearctic hirudisomatids are diagnosed by the broad telson, but this structure is narrower in *O. gracilipes* and subequal in breadth to that of species of *Polyzonium* (Figs. 12, 24). The collum overhangs the epicranium and the uppermost ocelli in hirudisomatids, but it likewise overlaps part of the head in some western polyzoniids and thus does not discriminate the families. The

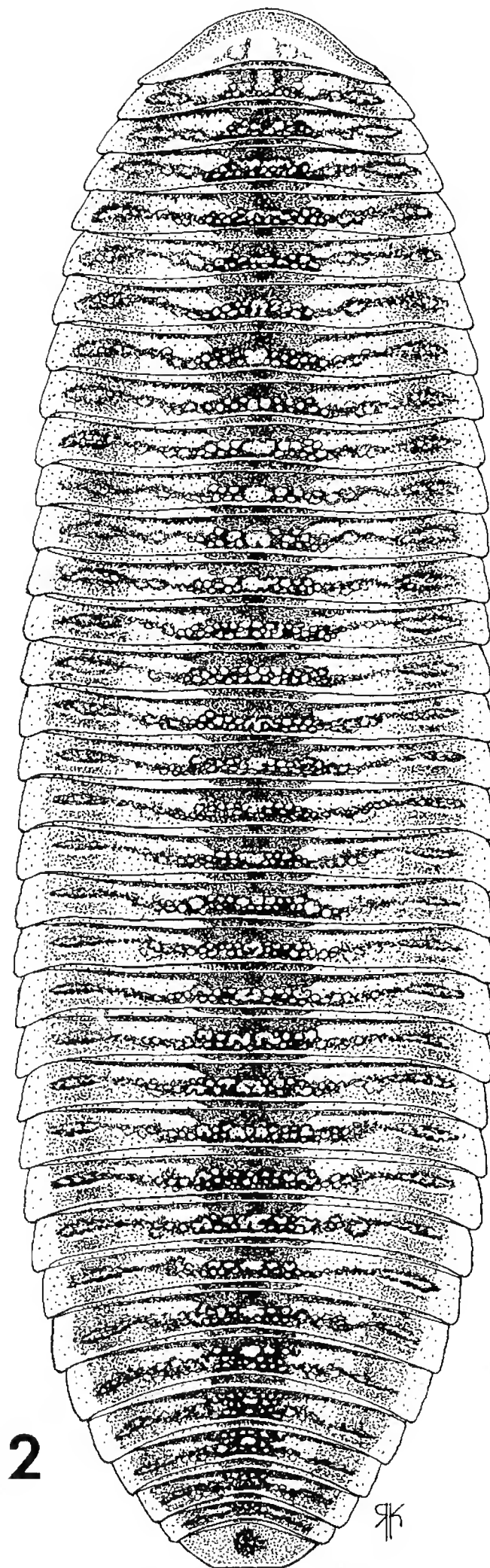


Fig. 2. *Octoglena bivirgata*. Dorsal view of female from Marin County, California. Scale line = 1.00 mm.

only inviolable characters involve the size and position of the penes on the second male coxae, which must be dissected and examined under a compound microscope. In his key to North American diplopod families, Hoffman (1990) placed the penes on the ventral coxal surface in the Hirudisomatidae and caudal to this podomere in the Polyzoniidae. To determine the correct family for *Mexiconium*, I had to examine the penes and compare their shape and location with these attributes in definite representatives of both families. As shown in figs. 3-4, the short, subconical penes of *M. absidatum* resemble those of *O. bivirgata*, and both are positioned caudoventrad on the coxae; in *Polyzonium rosalbum* (Cope), however, the structures are longer, "bottle shaped," and arise more dorsad (Fig. 5). Enghoff and Golovatch (1995) provide SEM photos of a European hirudisomatid and polyzoniid that also show the penes in these positions, so couplet 16a of Hoffman's key (1990) should be amended to read "caudoventrad" as to the location of the penes in the Hirudisomatidae.

Acronyms of sources of preserved study material are as follows:

AMNH—American Museum of Natural History, New York, New York.

CMN—Canadian Museum of Nature, Ottawa, Ontario,

FSCA—Florida State Collection of Arthropods, Gainesville.

NCSM—North Carolina State Museum of Natural Sciences, Raleigh.

NMNH—National Museum of Natural History, Smithsonian Institution, Washington, DC.

RBCM—Royal British Columbia Museum, Victoria.

VMNH—Virginia Museum of Natural History, Martinsville.

WAS—Private collection of William A. Shear, Hampden-Sydney, Virginia.

Literature Review

The history of the Hirudisomatidae in the New World begins with the proposal of *Octoglena* by Wood (1864) for *O. bivirgata*, a new species with fuscous stripes believed to inhabit the mountains of Georgia. He (Wood 1865) repeated these accounts and provided illustrations of the ventral and dorsal surfaces of the head. In the only other reference of the 19th century, Bollman (1893) included *Octoglena* in a key to North American myriapod genera.

In the twentieth century, Cook (1904) proposed *Hypozonium* for *H. anurum*, a new species from Seattle, King County, Washington, and Chamberlin (1911) recorded it from Bremerton, Kitsap County. Cook and Loomis (1928) reiterated these records and transferred *bivirgata* into *Polyzonium*, thereby relegating *Octoglena* to the generic synonymy,

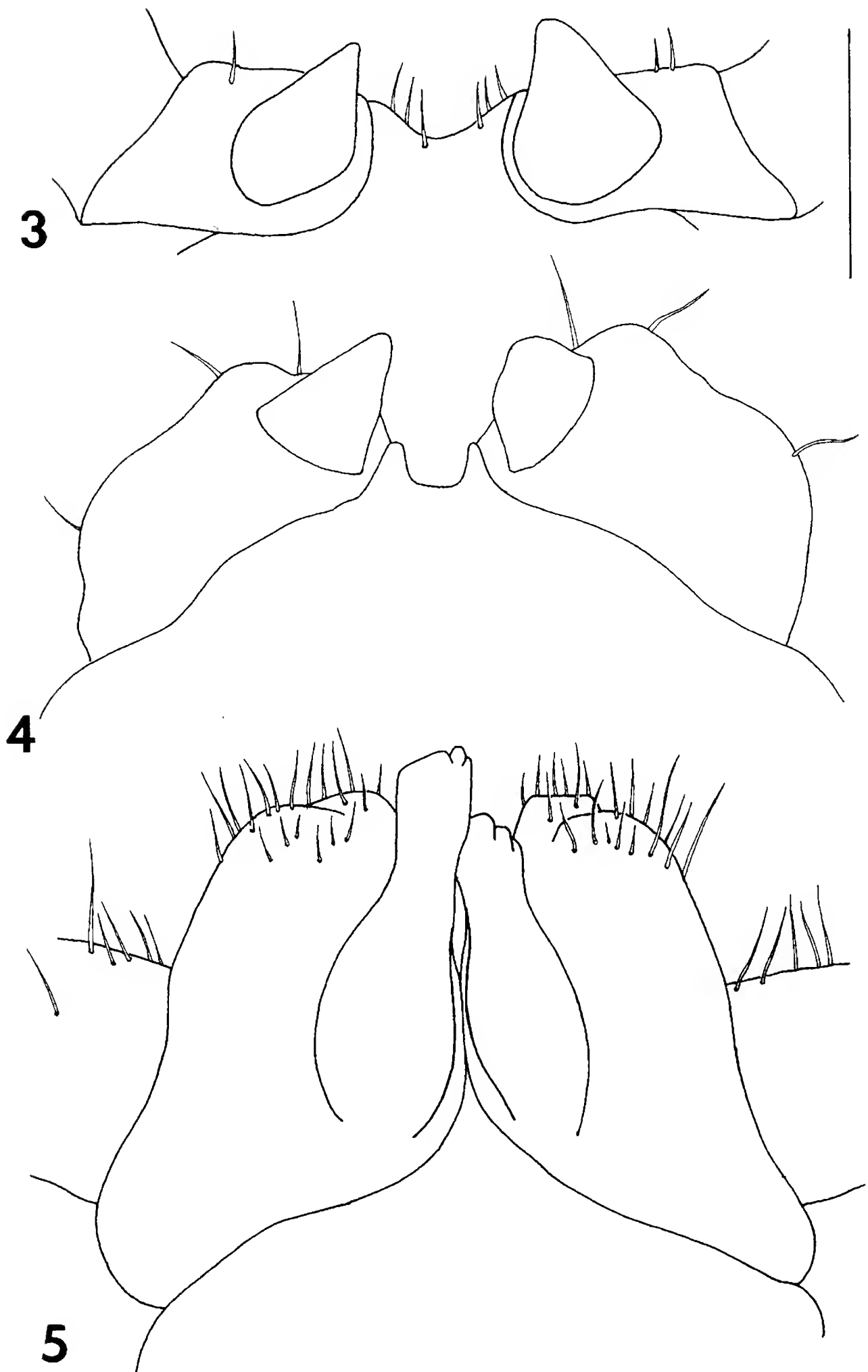
where it remained for 52 years. Chamberlin (1950) erected *Euzonium* for *E. crucis*, a striped species from Felton, Santa Cruz County, California, and (1954) proposed *Hypozoneum arnaudi*, for a striped female from this locality that was taken on the same date and by the same collector as the type of *E. crucis*. Chamberlin and Hoffman (1958) included *Octoglena* in the synonymy of *Polyzoneum* and reported *Euzonium*, *Hypozoneum*, *E. crucis*, and *H. anurum*, inadvertently omitting *H. arnaudi*. However, Buckett (1964) included this species in his listing of California diplopods, and Jeekel (1971) cited all the genera along with their type species. Hoffman (1980) assigned *Hypozoneum* and *Euzonium* to the Hirudisomatidae and revived *Octoglena* for a California hirudisomatid, because the collector, John Lawrence LeConte, sampled in California as well as Georgia, and because the striped pigment pattern fits Californian, rather than Georgian, polyzonioids. Hoffman (1980) and Shelley (1988) suggested that *O. bivirgata* Wood may be a senior name for *E. crucis* and *H. arnaudi*, which the present study confirms. Kevan (1983) reported *H. anurum* from unspecified sites in British Columbia, the first ordinal records from western Canada, and Kevan and Scudder (1989) included the milliped in their key to Canadian myriapods. Shelley (1990) reported five localities for *H. anurum* in the southwestern corner of the British Columbia mainland, which were reiterated by Scudder (1994).

Key to North American Families of the Polyzoniida
(adapted from that by Hoffman (1990))

- 1. Tarsal claws with prominent, overhanging paronychium; animals relatively quick and active, color pink; south Florida and Louisiana.
..... Siphonotidae
- Tarsal claws simple, without paronychium; animals relatively sluggish, color pale white, yellowish, or with one or three dark longitudinal stripes 2
- 2. Caudal edges of metaterga detached from succeeding tergite, elevated or variably upturned; telson broad or narrow; penes short and subconical, located caudoventrad on 2nd male coxae (Figs. 3-4, 8, 12) Hirudisomatidae
- Caudal edges of metaterga not upturned, smoothly overlying and closely appressed to succeeding tergite; telson narrow; penes relatively long, located well dorsad on caudal surface of 2nd male coxae (Fig. 5) Polyzoniidae

Family Hirudisomatidae
Genus *Octoglena* Wood

Octoglena Wood, 1864:186; 1865:229. Bollman, 1893:117, 137, 187.



Figs. 3-5. Comparison of penes, caudal views of 2nd male coxae. 3, *O. bivirgata*, Sonoma County, California. 4, *M. absidatum* holotype. 5, *Polyzonium rosalbum*, Dade County, Georgia. Scale line = 0.25 mm for all figs.

Jeekel, 1971:41. Hoffman, 1980:73.

Hypozonium Cook, 1904:62. Cook and Loomis, 1928:17. Chamberlin and Hoffman, 1958:187. Buckett, 1964:29. Jeekel, 1971:39. Hoffman, 1980:73. Kevan, 1983:2962. **NEW SYNONYMY.**

Euzonium Chamberlin, 1950:1. Chamberlin and Hoffman, 1958:187. Buckett, 1964:29. Jeekel, 1971:38. Hoffman, 1980:73. **NEW SYNONYMY.**

Type species—Of *Octoglena*, *O. bivirgata* Wood, 1864, by monotypy; of *Hypozonium*, *H. anurum* Cook, by monotypy; of *Euzonium*, *E. crucis* Chamberlin, 1950, by original designation.

Diagnosis—Dorsum granular, with or without three dark, longitudinal stripes; caudal metatergal margins detached from succeeding tergite, upturned to varying degrees, body broad (W/L ratio generally 28-38%), flattened “bell shaped” in profile, sides extending strongly laterad; collum broad, overhanging epicranium and at least one pair of ocelli; telson variable, either broad and comprising nearly entire caudal width, or relatively narrow and comprising around half of caudal width; head subtriangular, with three ocelli on each side arranged linearly in angular rows beginning at levels of antennal sockets; sternum of anterior gonopods with strong, apically hirsute lobes, segregated to varying degrees; anterior gonopods curving variably anteromediad distad, ultimate podomere divided, with broad, hirsute, ventral lobe of variable size usually overhanging dorsal glabrous branch, latter either short, broad, and apically blunt, curved slightly ventrad, and directed anteromediad, or long, narrow, and acuminate, slightly sinuate and directed sublaterad; corners of 4th and 5th podomeres extended on caudal side; coxa with or without hirsute anterior lobe, length variable; posterior gonopod with ultimate podomere simple and acicular, apically acuminate, fimbriate, or lightly hirsute, projecting anteriorly between solenomere and ventral lobe.

Species—Five.

Distribution—Along the Pacific Coast from the southwestern corner of the British Columbia mainland to central Santa Cruz County, California, extending inland to the western slope of the Cascade Mountains from British Columbia to central Oregon and the eastern slope of the Coast Range in southern Oregon and California, with a localized allopatric species some 75 mi (120 km) to the east in the Sierra Nevada foothills, Placer County, and one 1,897 mi (3,035 km) farther east in the eastern United States, extending from westcentral South Carolina to southcentral Tennessee and northwestern Alabama (Figs. 1, 28-29). The coastal species are contiguous and demonstrate parapatric spatial relationships and a sublinear, north to south, arrangement, the area being wider from central Oregon northward. Dimensions are approximately 850

mi (1,360 km), north/south, and 110 mi (176 km), east/west, for the coastal area, and 220 mi (352 km), north/south, and 380 mi (608 km), east/west, for the eastern.

Relationships—With the somatic differences and the apomorphic absence of the coxal lobe, *O. gracilipes* is sister to the western species (Fig. 30). *Octoglena sierra* is sister to those along the Pacific Coast, which share the configuration of the ultimate anterior gonopod podomere, and *O. anura*, with the short, apically linear coxal lobe, is sister to *O. prolata* plus *O. bivirgata*, in which the lobe is extended and apically rounded.

Remarks—The anterior gonopods of each species are quite uniform and show little intraspecific variation, so I analyze segment numbers and lengths of measurable specimens in the variation sections. As per the recommendation of Enghoff et al. (1993), I exclude the telson from the segment counts.

Key to Species of *Octoglena*

1. Caudolateral corners of midbody metatergites slightly but distinctly extended and rounded; telson broad, extending for nearly entire breadth of caudal extremity; anterior gonopod coxae with hirsute lobes of varying lengths (Figs. 9, 13, 16, 19); southwestern British Columbia to central California 2
- Caudolateral corners of midbody metatergites not extended, continuous with middorsal margins, apically blunt; telson narrow, comprising no more than half of breadth of caudal extremity; anterior gonopod coxae without lobes (Fig. 25); North and South Carolina to Tennessee and Alabama..... *gracilipes* (Loomis)
2. Ultimate podomere of anterior gonopod with broad, distinct lobe ventral to and overhanging dorsal glabrous branch; latter relatively short and broad, curved slightly ventrad, directed antero-medial (Figs. 9, 13, 16); along Pacific Coast from British Columbia to Santa Cruz County, California 3
- Ultimate podomere of anterior gonopod with at most short, indistinct, ventral lobe, not overhanging dorsal branch; latter relatively long and narrow, slightly sinuate, directed sublateral (Fig. 19); western Placer County, California *sierra*, new species
3. Coxal lobe of anterior gonopod short and apically sublinear, not overlying distal podomeres; ultimate podomere of posterior gonopod apically narrow and with numerous short hairs (Figs. 13, 15); southwestern British Columbia to northern Douglas County, Oregon *anura* (Cook)

- Coxal lobe of anterior gonopod long and apically rounded, overlying distal podomeres; ultimate podomere of posterior gonopod apically fimbriate (Figs. 9, 11, 16, 18) 4
4. Coxal lobe of anterior gonopod leaning slightly mediad, barely overlapping distal podomeres; dorsum pigmented, with three dark, longitudinal stripes (Figs. 2, 9); Curry County, Oregon, to Santa Cruz County, California *bivirgata* Wood
- Coxal lobe of anterior gonopod leaning strongly laterad, clearly overlapping distal podomeres; dorsum pale yellow to white, without stripes (Fig. 19); Douglas, Jackson, and Josephine counties, Oregon *prolata*, new species

Octoglena bivirgata Wood

Figs. 2, 3, 6-11

Octoglena bivirgata Wood, 1864:186; 1865:229-230, figs. 58-59. Bollman, 1893:117, 187.

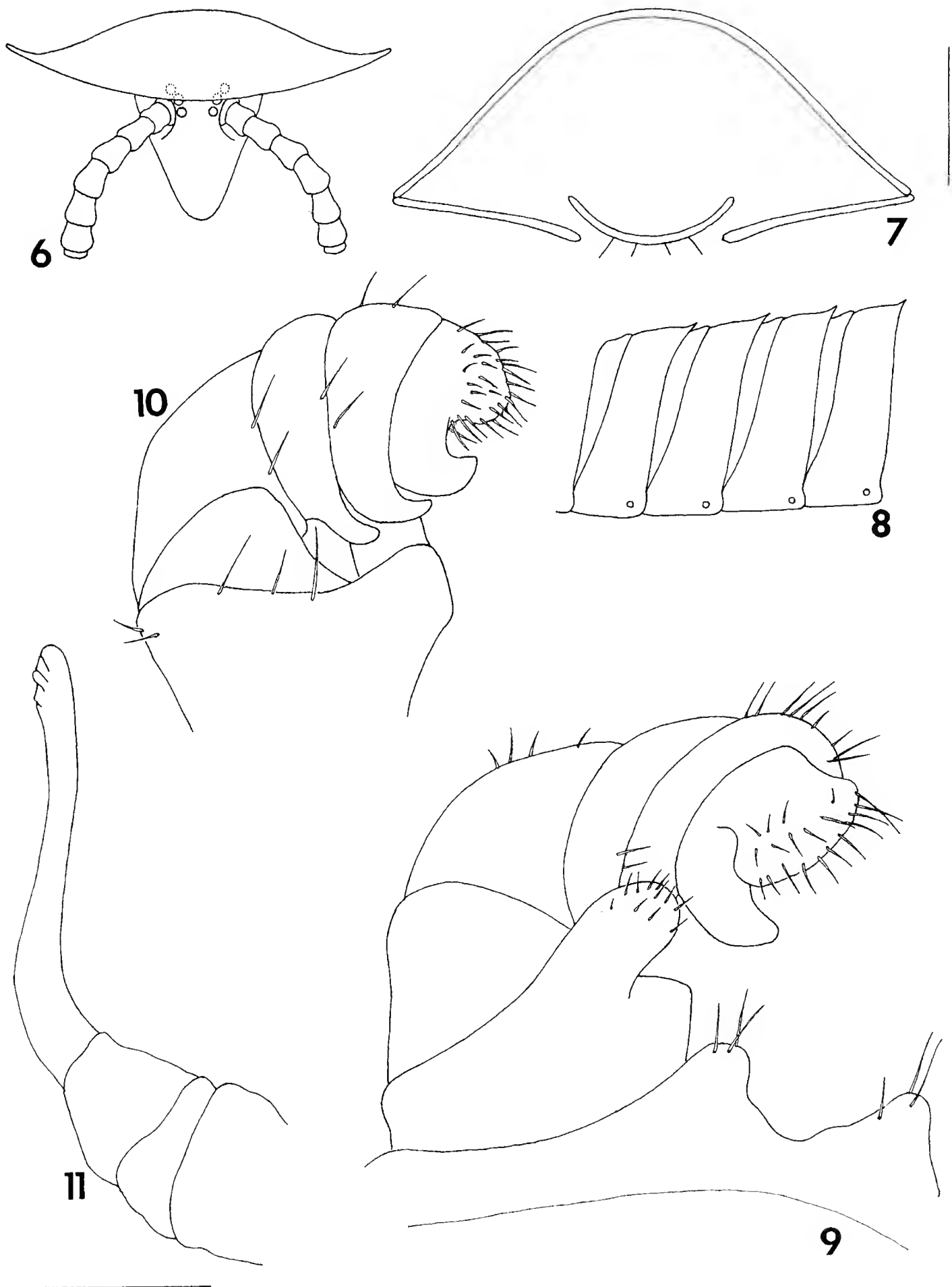
Euzonium crucis Chamberlin, 1950:1-2. Chamberlin and Hoffman, 1958:187. Buckett, 1964:29. **NEW SYNONYMY.**

Hypozonium arnaudi Chamberlin, 1954:233. Buckett, 1964:29. **NEW SYNONYMY.**

Type specimens—Male neotype (AMNH) collected by V. Roth, 19 July 1962, 2 mi (3.2 km) N Ft. Ross, along California highway 1, ca. 15.3 mi (24.5 km) N Bodega Bay, Sonoma County, California.

Citing a letter from R. L. Hoffman, Loomis (1971:155) reported that the type, which lacked the anterior end, was at the Academy of Natural Sciences, Philadelphia (ANSP), but extensive searches in June 1995 by the entomology collection manager failed to locate it. The specimen therefore appears to be lost, and neotype designation is needed to stabilize the name, necessitating library research on the collector, the entomologist and medical doctor, John Lawrence LeConte, and the origin of the confusion between Georgia and California.

In the original accounts, Wood (1864, 1865) indicated uncertainty about the type locality by stating that he *believed* it to be the mountains of Georgia. That the site was probably in California is shown by unquestionable California material, collected by LeConte, that incorrectly carries a Georgia label. For example, Chamberlin (1947) reported several ANSP males of the California genus *Xystocheir* Cook (Polydesmida: Xystodesmidae) that were taken by LeConte and erroneously labeled "Georgia." Wood (1867) explained that LeConte collected in both Georgia and California, that he presented all of his material to the ANSP, but that there was only one bottle, labeled Georgia. Thus, Wood originally concluded that the California specimens were missing,



Figs. 6-11. *O. bivirgata*, neotype. 6, head and collum, anterior view, setation and pigmentation omitted. 7, profile of midbody segment, caudal view. 8, midbody segments, lateral view of left side, pigmentation omitted. 9, left anterior gonopod and sternum, anterior view. 10, right anterior gonopod, caudal view. 11, left posterior gonopod, caudal view. Upper scale line = 0.50 mm for figs 6-8; lower line = 0.25 mm for figs 9-11.

but he later realized that they were probably combined with the Georgia material. According to Horn (1884*a, b*), LeConte visited California in 1850, staying in San Francisco, San Jose, and San Diego, after which he traveled to central Arizona. He then returned to California and New York, moving to Philadelphia in 1852. Consequently, the only places where LeConte is likely to have collected in California were around these cities, and San Diego is eliminated as a potential site because of its aridity. Polyzonoids do not occur nearly this far south, the southernmost hirudisomatid record being from central Santa Cruz County, some 330 mi (528 km) to the north. The original material therefore probably came from the vicinities of San Francisco and/or San Jose, which are within the ranges of the family and the striped species.

Diagnosis—Dorsum with dark medial and two lighter lateral stripes; caudal metatergal margins strongly upturned, caudolateral corners of midbody metatergites slightly but distinctly extended and rounded; telson broad, comprising entire breadth of caudal extremity; sternal lobes of anterior gonopods relatively short, moderately segregated; coxal lobe of latter moderately long and broad, apically rounded, leaning mediad and overlapping corners of 4th and 5th podomeres; dorsal branch of ultimate podomere short and broad, apically blunt, curved slightly ventrad and directed submediad; ventral lobe of ultimate podomere distinct, clearly overhanging dorsal branch; ultimate podomere of posterior gonopod apically fimbriate (Figs. 2, 6-11).

Variation—Males with seemingly mature gonopods have from 21 to 55 segments and vary in length from 2.8 to 19.1 mm; female segment numbers vary from 12 to 58, while lengths range from 1.6 to 19.7 mm. These data are presented in table 1, with localities arranged in a general north to south sequence. Individuals are slightly longer toward the south of the range.

Ecology—Habitat notations on vial labels include “under wet, rotting branches,” “redwood litter,” “under a piece of redwood log,” “on a redwood stump,” and “under rock on damp, muddy floor” in a cave.

Distribution—The southernmost western species, *O. bivirgata* traverses San Francisco Bay and extends from coastal Curry County, Oregon, to central Santa Cruz County, California; although primarily hugging the coastline, the distribution extends eastward to the eastern slope of the Coast Range in western Colusa County (Fig. 28). Maximum dimensions are around 385 mi (616 km), north/south, and 67 mi (107 km), east/west. Specimens were examined as follows; the initials AKJ in this and the succeeding account denote samples collected by

Table 1. Segment Numbers and Average Lengths (mm) of *O. bivirgata* (samples at one locality are combined; lengths averaged for individuals with same segment number, n in parentheses).

County	Locality	Males		Females	
		Segs.	Lengths	Segs.	Lengths
Humboldt, CA	2 mi E	55	19.1	58	19.7
	Trinidad	46	12.2	51	15.3
Humboldt, CA	2.5 mi S Blue Lake	49	15.6		
Humboldt, CA	Arcata	44	13.2	(2) 50	14.8
		43	12.3	49	15.0
		42	11.9	41	9.2
		(2) 38	8.7		
		37	8.2		
Humboldt, CA	2.75 mi NE	50	12.4	52	16.9
	Orleans	(2) 45	11.0	48	12.8
		41	9.1	45	15.3
		34	5.4	39	9.1
		28	4.7	38	8.3
				36	7.1
Humboldt, CA	11 mi W Willow Creek			41	9.1
Humboldt, CA	3.5 mi "up" Fickle Hill Rd.			41	15.1
Humboldt, CA	Redcrest	(2) 43	11.9	34	8.7
		(2) 39	11.6	33	8.2
		33	7.3	(2) 24	4.4
		30	5.3	(2) 23	4.3
		28	5.0	(3) 18	2.6
				17	2.5
				12	1.7
Humboldt, CA	4.5 mi N	41	10.3	40	11.6
	Pepperwood	39	9.8	38	11.2
		24	4.0	37	9.1
				36	8.1
				34	7.0
Humboldt, CA	Weitchpec	(3) 40	9.7	40	9.0
		39	9.0	39	9.5

Table 1. Continued.

County	Locality	Males		Females	
		Segs.	Lengths	Segs.	Lengths
		27	4.6	(2) 27	4.7
		(2) 25	4.3	(3) 26	4.5
				(2) 25	4.0
				24	3.7
				(2) 23	3.7
				17	2.3
				12	1.6
Mendocino, CA	Elk			37	10.2
Mendocino, CA	12.7 mi SSW Leggett	(2) 35	9.9	42	14.0
		(2) 34	9.3	39	12.0
		33	9.5	(2) 37	11.9
		32	8.1	36	12.9
		30	7.7	(4) 35	11.0
		29	6.5	(2) 34	9.9
		27	6.5	(4) 33	9.2
				(4) 32	8.4
				(6) 31	8.2
				29	6.9
				28	6.0
				27	6.8
Lake, CA	Kelsey Cr.	32	6.5	33	7.9
Colusa, CA	2 mi W jct. Hys. 20 & 16			34	6.0
Sonoma, CA	El Verano	36	10.2	38	11.1
Sonoma, CA	2 mi N Ft. Ross	32	6.3		
Napa, CA	Clay Cave			44	13.7
Marin, CA	Bollinas Jct.	36	7.8	34	8.9
		30	6.0	33	6.8
				32	6.3
				30	5.6
Marin, CA	Inverness Ridge	27	6.8	30	8.0
				29	5.7

Table 1. Continued.

County	Locality	Males		Females	
		Segs.	Lengths	Segs.	Lengths
Marin, CA	1 mi S Inverness			35	9.6
Marin, CA	2 mi SSW Inverness	29	5.8		
Marin, CA	Lagunitas Cyn.			(2) 37	11.4
Marin, CA	Sam P. Taylor St. Pk.	32	7.7	(3) 34	9.5
		(3) 31	8.0	33	9.5
		29	7.1	32	9.3
Marin, CA	Mt. Tamalpais			40	9.7
San Mateo, CA	6.5 km ESE Half Moon Bay			30	6.1
Santa Clara, CA	Stevens Cr.	29	6.0	35	7.7
		(2) 28	6.3	34	7.1
				(2) 33	8.4
				32	7.3
				31	6.5
				29	5.8
				28	6.1
				26	6.4
				(2) 25	5.0
				24	4.7
Santa Cruz, CA	9.5 mi NE Soquel	(2) 31	6.6	32	7.7
		29	6.3	30	5.7
		26	4.5	29	5.8
		25	4.6	19	3.2
		21	2.8		

A. K. Johnson.

OREGON: *Curry Co.*, Gold Beach, M, 19 August 1961, W. Suter (FSCA).

CALIFORNIA: *Colusa Co.*, 2 mi (3.2 km) W jct. hwys. 20 & 66, F, juv., 30 November 1960, T. Fenner (FSCA). *Del Norte Co.*, 2 mi (3.2 km) N, 7 mi (11.2 km) E Gasquet, Cedar Rustic Cpgd.,

3M, 22 December 1977, AKJ (VMNH); 7 mi (11.2 km) ENE Gasquet, Patrick Cr. Cpgd., 3M, 5F, 22 December 1977, AKJ (VMNH); 5 mi (8 km) E Gasquet, Grassy Flat Cpgd. along CA hwy. 199, M, 25 March 1976, AKJ (VMNH); and Gasquet, M, 1 November 1977, and M, 2F, 22 December 1977, AKJ (VMNH). *Humboldt Co.*, Arcata, Humboldt St. Univ., Fern L. vic., 2F, 25 January 1976, AKJ (VMNH); Redcrest, 7M, 3F, 5 juvs., 25 November 1977, AKJ (VMNH); Tish Tang Rec. Area, along CA hwy. 299 N Willow Creek (town), 4M, F, 21 February 1976, and 2F, 20 December 1979, AKJ (VMNH); 11 mi (17.6 km) W Willow Creek, M, 2F, 28 March 1976, AKJ (VMNH); Cheatham Redwood Grove, along CA hwy. 36 at Van Duzen R., F, 19 December 1977, AKJ (VMNH); 2.75 mi (4.4 km) NNE Orleans, MM, FF, juvs., 21 December 1976, AKJ (VMNH); 4.5 mi (7.2 km) N Pepperwood, along CA hwy. 36, 5M, 5F, 2 juvs., 12 November 1977, AKJ (VMNH); 3.5 mi (5.6 km) N, 1 mi (1.6 km) E Pepperwood, along CA hwy. 36, F, 12 November 1977, AKJ (VMNH); Big Lagoon, M, 30 November 1974, AKJ (VMNH); 1.5 mi (2.4 km) S Scotia, along US hwy. 101, M, juv., 3 January 1977, AKJ (VMNH); 3.5 mi (5.6 km) "up" Fickle Hill Rd., F, 29 November 1975, W. B. Dean (VMNH); 1.5 mi (2.4 km) NE, 1.75 mi (2.8 km) SE Orick, along Redwood Cr., 2M, F, 27 November 1976, and F, juv., 26 March 1977, AKJ (VMNH); 5 mi (8 km) E, 2.5 mi (4 km) S Blue Lake, along Canon Cr., M, F, 5 February 1976, AKJ (VMNH); 2 mi (3.2 km) E Trinidad, 2M, 9 March 1976, G. Panting (VMNH); Patrick's Pt. St. Pk., M, 2F, 7 December 1974, AKJ (VMNH); Redwood Nat. Pk., Bald Hills Rd., M, 27 March 1977, AKJ (VMNH); and Weitchpec, along Klamath R., MM, FF, 30 November 1974, AKJ (VMNH). *Lake Co.*, Cobb Mtn., along Kelsey Cr., 2F, 13 March 1962, J. S. Buckett (FSCA). *Marin Co.*, Bolinas Jct., 2M, 4F, 29 September 1965, W. Ivie (AMNH); Inverness Ridge, 2M, 2F, 9 October 1963, J. S. Buckett (FSCA); 1 mi (1.6 km) S Inverness, F, 21 March 1959, C. W. O'Brien (FSCA); 2 mi (3.2 km) SSW Inverness, F, 30 December 1961, J. S. Buckett (FSCA); Lagunitas Cyn., 2F, 7 April 1946, H. P. Chandler (FSCA); Sam P. Taylor St. Pk., M, 28 September 1959, J. Wagner (FSCA) and 2M, 5F, 19 September 1962, N. B. Causey (FSCA); and Mt. Tamalpais St. Pk., F, 1 April 1958, Lange (VMNH). *Mendocino Co.*, 12.7 mi (20.3 km) SW Leggett, along CA hwy. 208, MM, FF, 21 March 1976, G. & J. Parkinson, AKJ (VMNH); 4 mi (6.4 km) S Rockport, F, 19 August 1959, V. Roth (NMNH); 1 mi (1.6 km) SE Caspar, M, 13 September 1961, W. J. Gertsch, W. Ivie (NMNH); along Little R., 3 August 1957, F, juv., 3 August 1957, J. R. Helfer, G. A. Marsh (NMNH); and Elk, F, 16 February 1967, V. Roth (AMNH).

Napa Co., Clay (Kiel) Cave, 3 mi (4.8 km) N St. Helena, F, 26 November 1959, R. Graham (FSCA). *San Mateo Co.*, 6.5 mi (10.4 km) ESE Half Moon Bay, along Purisima Cr., juv., 25 December 1974, AKJ (VMNH); 6 mi (9.6 km) SE Half Moon Bay, 2M, 3F, 1 June 1957, juv., 21 July 1957, R. O. Schuster (NMNH); and Woodside, M, 2F, 18 January 1947, P. H. Arnaud (NMNH). *Santa Clara Co.*, along Stevens Cr., M, 14F, 2 June 1957, R. O. Schuster (NMNH, VMNH). *Santa Cruz Co.*, Felton, F, 6 February 1949, P. H. Arnaud (NMNH); and 9.5 mi (15.2 km) NE Soquel, 5M, 4F, 31 December 1956, S. M. Fidel (VMNH). *Sonoma Co.*, 2 mi (3.2 km) N Ft. Ross, M, 19 July 1962, V. Roth (AMNH) NEOTYPE LOCALITY; and El Verayo, along Fowler Cr., exact location unknown, 2F, 29 November 1975, J. DeMartini (VMNH).

Remarks—The holotype of *E. crucis* is lost, and its sex is unknown, as Chamberlin (1950) merely states that there was “one specimen.” The female holotype of *H. arnaudi*, collected at the same time and place, and by the same collector, is available and confirms Hoffman’s (1980) and Shelley’s (1988) beliefs that both names are synonyms of *O. bivirgata*. It displays the diagnostic striped color pattern (Fig. 2), and the gonopods of proximate males agree with those of males from throughout the range of the striped species.

Unlike most diplopod pigmentations, the stripes of *O. bivirgata* persist and are usually visible after 30-40 years in alcohol. Occasional specimens are pallid or nearly so, displaying only a trace of the stripes, but most individuals of *O. bivirgata* can be distinguished from sympatric polyzonoids by this distinctive pattern.

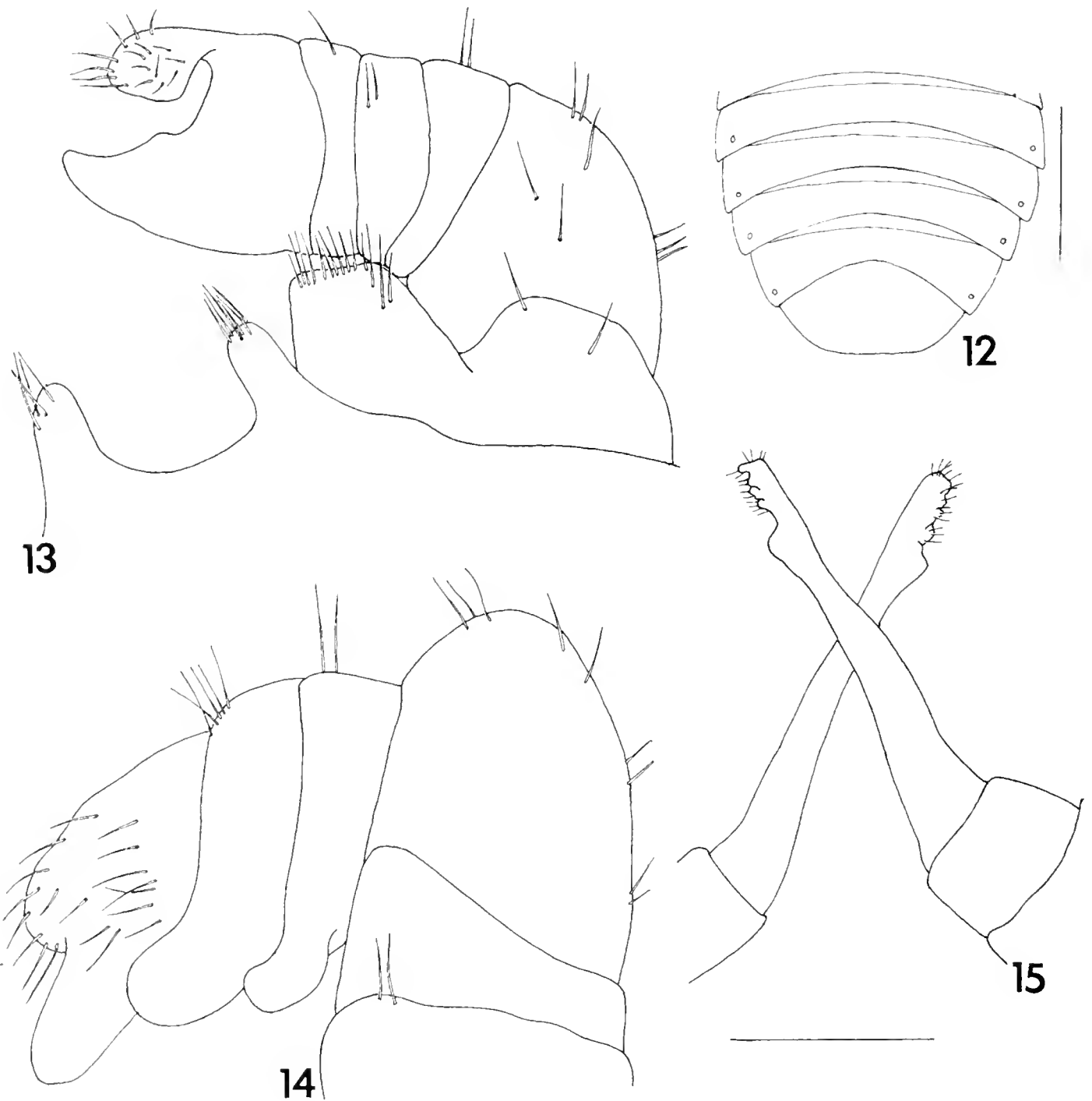
Octoglena anura (Cook), new combination

Figs. 12-15

Hypozonium anurum Cook, 1904:63, pl. V, figs. 1a-d. Chamberlin, 1911:262. Cook and Loomis, 1928:17. Chamberlin and Hoffman, 1958:187. Kevan, 1983:2962. Scudder, 1994:22.

Type specimens—The holotype, from Seattle, Washington, was type no. 791 at the NMNH (Cook 1904, Chamberlin and Hoffman 1958), but it is now lost. Male neotype and female paraneotype (FSCA) collected by W. Suter, 15 August 1961, in Saltwater State Park, ca. 18 mi (28.8 km) S Seattle, King County, Washington.

Diagnosis—Dorsum without stripes, color pale yellow to white; caudal metatergal margins indistinctly upturned, caudolateral corners of midbody metatergites slightly but distinctly extended and rounded; telson broad, comprising entire breadth of caudal extremity; sternal lobes of anterior gonopods relatively long, widely segregated; coxal



Figs. 12-15. *O. anura*, neotype. 12, telson and caudal tergites, dorsal view. 13, right anterior gonopod and sternum, anterior view. 14, left anterior gonopod, caudal view. 15, ultimate podomeres of posterior gonopods, caudal view. Scaleline for fig. 12 = 1.00 mm; line for other figs. = 0.25 mm for each.

lobe of latter short, broad, and upright, apically linear, not overlapping distal podomeres; dorsal branch of ultimate podomere short and broad, apically blunt, curved slightly ventrad and directed submediad; ventral lobe of ultimate podomere distinct, clearly overhanging dorsal branch; ultimate podomere of posterior gonopod narrowing apically, lightly hirsute (Figs. 12-15).

Variation—Males with seemingly mature gonopods have from 16 to 40 segments and vary in length from 3.4 to 13.3 mm, the latter, a specimen with 38 segments, being slightly longer than that with

Table 2. Segment Numbers and Average Lengths (mm) of *O. anura* (samples at one locality are combined; lengths averaged for individuals with same segment number, n in parentheses).

County	Locality	Males		Females	
		Segs.	Lengths	Segs.	Lengths
BC	1.9 mi SE Hope	28	8.3	30	9.4
		(2) 25	6.1	26	6.9
		24	5.7	25	6.1
		23	4.9	(2) 24	5.8
		22	5.6	(3) 23	5.9
		19	4.1	22	5.0
				19	3.7
				(2) 18	3.9
				(2) 14	2.6
BC	Manning Prov. Pk.	26	6.4	26	7.1
		22	4.4	25	5.5
Clallam, WA	Olympic Hot Spgs.	27	6.5	27	5.0
		25	5.1	24	4.8
		23	4.0		
Jefferson, WA	5.5 mi S Brinnon	34	9.1	27	7.1
		31	8.0	(2) 26	7.0
		29	8.8		
		(5) 27	6.8		
		26	6.0		
		25	6.0		
		23	5.5		
Mason, WA	Kamilche Pt.	40	12.9	21	4.3
		25	6.0		
		22	5.0		
King, WA	Federation For. St. Pk.			32	9.3
King, WA	Saltwater St. Pk.	25	5.7	31	8.6
Thurston, WA	Puget	28	7.3	30	7.0
		25	6.1	29	7.1
				25	6.4
Pierce, WA	Mt. Rainier Nat. Pk.	22	5.0	29	8.1

Table 2. Continued.

County	Locality	Males		Females	
		Segs.	Lengths	Segs.	Lengths
Cowlitz, WA	1 mi E Touttle	31	9.4		
Multnomah, OR	Portland	(2) 28	7.1	31	6.7
		27	6.7		
		25	5.6		
		24	5.7		
Washington, OR	5 mi SW	29	8.1	28	6.9
	Tualatin	28	6.5		
Clackamas, OR	10 mi E Zigzag	30	8.0	29	9.0
		28	7.5	(2) 28	8.1
		(2) 26	6.7	(2) 26	6.7
		25	6.2	(2) 25	7.0
		(4) 24	5.9	24	5.6
		(2) 23	5.2	(6) 23	5.4
		22	5.9	21	4.9
		(2) 20	4.3	20	3.8
		19	4.0	19	4.4
		(2) 18	3.5	(2) 16	2.9
		(2) 16	2.9	14	2.4
Yamhill, OR	5 mi E	34	9.3		
	Yamhill	(2) 28	7.1		
Lincoln, OR	0.6 mi NW	29	9.3	28	8.2
	Elk City	28	7.6	27	8.6
				22	5.3
Benton, OR	6 mi N Corvallis	28	6.8	(2) 28	6.9
		27	6.9	27	5.8
		(2) 24	5.8	26	6.0
		(4) 23	5.4	25	5.5
		(2) 22	4.1	24	4.8
		21	4.4	(3) 23	5.1
		(6) 19	3.2	21	4.3
		(4) 18	3.3	20	3.5
		(2) 17	3.1	19	3.3
		16	3.4	(4) 18	3.3
				(5) 17	3.0
				16	2.8
				(4) 13	2.1
				(3) 12	2.0
				9	1.5
				(5) 5	1.0

Table 2. Continued.

County	Locality	Males		Females	
		Segs.	Lengths	Segs.	Lengths
Lane, OR	11 mi NE Blue R.	38	13.3		
Lane, OR	18.5 mi ESE Springfield	31	8.4		
		30	9.8		
		(4) 28	7.5		
		25	5.9		
Douglas, OR	Comstock	34	10.0	32	9.6

40 segments, which is 12.9 mm. Female segment numbers vary from 5 to 22, while lengths range from 1.0 to 9.6 mm. These data are presented in table 2, with localities arranged in a general north to south sequence. Lengths appear roughly comparable throughout the range, and no geographic trends are evident.

Ecology—The neotype was recovered from maple litter; habitat notations on labels in other vials include “under moss on forest floor,” “berlese conifer duff,” “willow, maple, fir duff, moss,” “in littler under firs, cedars,” “deciduous litter, grass,” “under log,” “bark, moss, debris,” “ash, oak, conifer duff,” “oak litter, rotted wood,” and “berlese beach grass debris, dried seaweed, spruce duff.”

Distribution—The northernmost species, *O. anura* extends along the Pacific Coast from the southwestern corner of the British Columbia mainland to northern Douglas County, Oregon, and ranges inland to the western slope of the Cascade Mountains (Fig. 28); dimensions are approximately 385 mi (616 km), north/south, and 110 mi (176 km), east/west, the former being about the same distance as the north/south dimension of *O. bivirgata*. Specimens were examined as follows; to consolidate records, I repeat the five from British Columbia cited by Shelley (1990). The initials EMB in this and the following account denote samples collected by E. M. Benedict, primarily from berlese extracts.

CANADA: BRITISH COLUMBIA: Burnaby Mtn., Simon Fraser Univ., 2M, 2F, 1972, R. G. Holmberg (CMN); Burquitlam, F, 10 March 1940, W. Dale (NMNH); Steelhead, F, 2 June 1933, H. B. Leech (NMNH); Agassiz, F, 7 March 1931, H. B. Leech (NMNH); 1.9 mi (3 km) SE Hope, Silver Skagit Rd., 8M, 13F, 4 juvs., 30 June 1988, S. & J. Peck (NCSM); and Manning Prov. Pk., West Gate, 2M, 2F,

1 July 1988, S. & J. Peck (NCSM).

USA: WASHINGTON: *Clallam Co.*, Olympic Hot Spgs., 3M, 2F, 15-16 August 1961, W. Suter (FSCA). *Cowlitz Co.*, 1 mi (1.6 km) E Toutle, M, F, 4 juvs., 16 April 1960, B. D. Ainscough (RBCM). *Jefferson Co.*, 5.5 mi (8.8 km) S Brinnon, along US hwy. 101, 9M, 4F, 23 September 1978, AKJ (VMNH). *King Co.*, Federation Forest St. Pk., F, 28 August 1990, R. M. Shelley (NCSM); and 18 mi (28.8 km) S Seattle, Saltwater St. Pk., M, F, 15 August 1961, W. Suter (FSCA) NEOTYPE LOCALITY. *Mason Co.*, Kamilche Pt., 3M, F, 25 November 1967, EMB (WAS). *Pierce Co.*, Mount Rainier Nat. Pk., Longmire Cpgd., M, F, 18 August 1961, W. Suter (FSCA). *Thurston Co.*, Puget, 2M, 3F, 28 October 1967, EMB (WAS); and Millersylvania St. Pk., M, 28 October 1967, EMB (WAS).

OREGON: *Benton Co.*, 6 mi (9.6 km) N Corvallis, McDonald For., F, 23 October 1969, 17M, 14F, 12 juvs., 21 February 1971, and 2M, 4F, 20 juvs., 21 February 1973, L. Russell (VMNH); and Mary's Peak, M, 30 October 1972, L. Russell (VMNH). *Clackamas Co.*, 10 mi (16 km) E, 3.5 mi (5.6 km) S Zigzag, Still Cr. Cpgd., 19M, 23F, 14 September 1977, AKJ (VMNH). *Clatsop Co.*, Ft. Stevens St. Pk., M, 22 November 1971, EMB (WAS). *Columbia Co.*, Locoda Sta. nr. Clatskanie, M, 2F, juv., 31 March 1937, J. Schuh (NMNH); and Scappoose, M, 7 May 1937, J. C. Chamberlin (NMNH). *Douglas Co.*, 6 mi (9.6 km) S Cottage Grove, 3M, 4F, 28 April 1937, J. C. Chamberlin (NMNH); Comstock, M, F, 7 January 1950, V. Roth (VMNH); 1 mi (1.6 km) SE Tiller, along Elk Cr. on OR hwy. 227, 6M, 3F, 6 November 1971, EMB (WAS); and 3 mi (4.8 km) SE Tiller, Umpqua R. Val., along OR hwy. 227, F, 6 November 1971, EMB (WAS). *Lane Co.*, 18.5 mi (29.6 km) ESE Springfield, Dolly Varden Cpgd. in Willamette Nat. For., along USFS 18, ca. 10 mi (16 km) E Fall Creek (town), 7M, 4 March 1972, EMB (WAS); and 11 mi (17.6 km) NE Blue River, Andrews Exp. For., M, 18 October 1983, C. L. Parsons (VMNH). *Lincoln Co.*, Saddlebag Mtn., ca. 14.5 mi (23.2 km) ENE Lincoln, 2F, 3 March 1960 & 6 January 1961, J. C. Dirks-Edmunds (FSCA); and 0.6 mi (1.0 km) NW Elk City, along Yaquina R., 2M, 3F, 20 December 1971, EMB (WAS). *Multnomah Co.*, Portland, Lewis & Clark Col., 2M, 11 May 1957, R. Ennis, M, F, March 1961, R. Anderson, and 3M, 1 May 1968, A. Ashwanden (FSCA). *Washington Co.*, 3 mi (4.8 km) SW Tualatin, 2M, F, 1 January 1972, EMB (WAS). *Yamhill Co.*, 5 mi (8 km) E Yamhill, along OR hwy. 240, M, 2 October 1971, EMB (WAS).

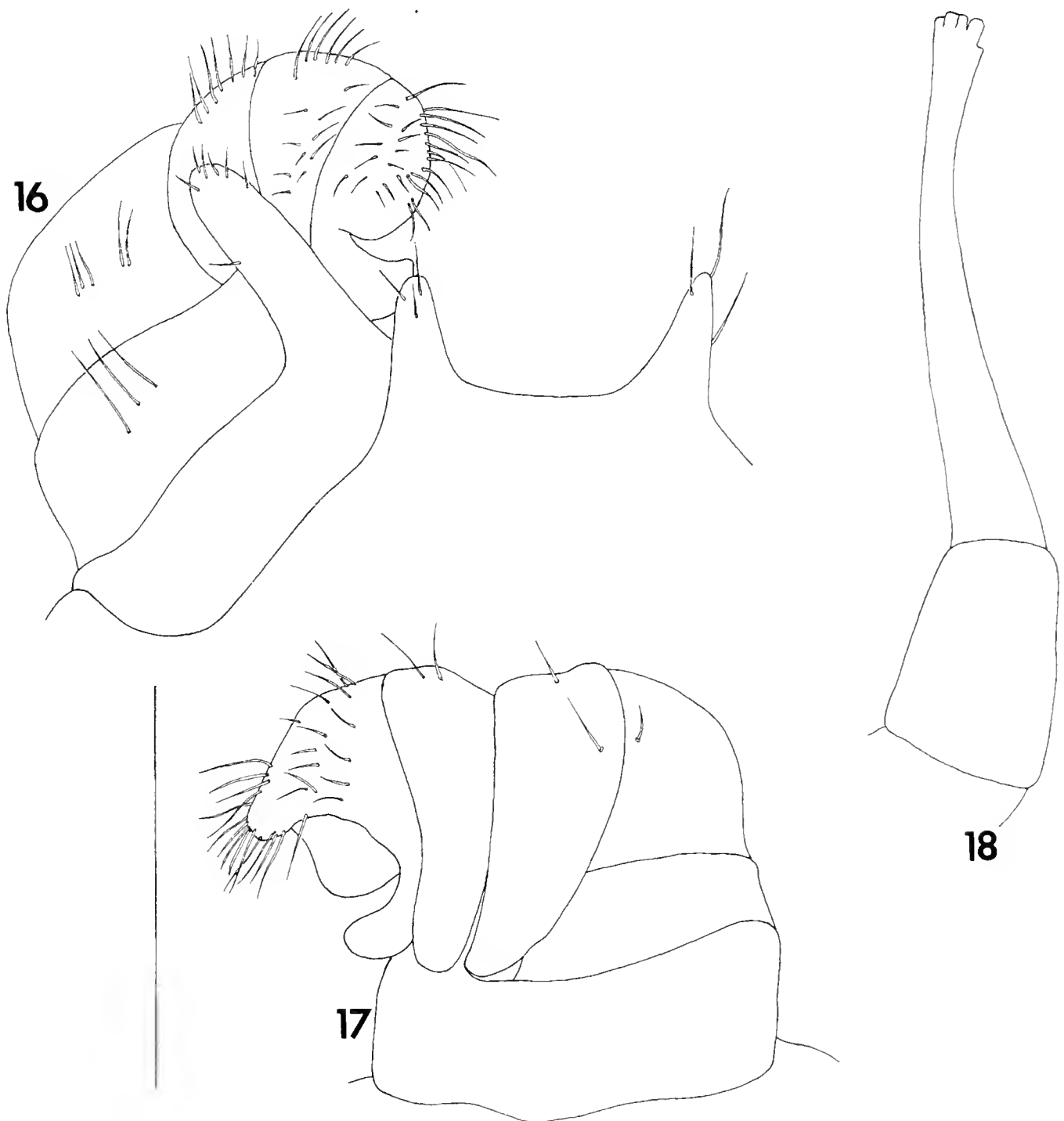
Literature Record: WASHINGTON: *Kitsap Co.*, Bremerton (Chamberlin 1911).

Remarks—Cook (1904) provided few clues as to this species' identity, but his illustration of the broad telson indicates a hirudisomatid, and only one ordinal representative, a hirudisomatid, occurs around Seattle and Puget Sound. It must therefore carry Cook's name.

Octoglena prolata, new species

Figs. 16-18

Type specimens—Male holotype and 3 male and 2 female paratypes (NMNH) collected by E. M. Benedict, 6 November 1971, along Oregon highway 227 in Canyonville, Douglas County, Oregon; 4 male and



Figs. 16-18. *O. prolata*, holotype. 16, left anterior gonopod and sternum, anterior view. 17, the same, caudal view. 18, distal podomeres of right posterior gonopod, caudal view. Scale line = 0.50 mm for all figs.

one female paratypes (VMNH) taken by same collector on same date in Canyonville County Park, 2 mi (3.2 km) E Canyonville.

Diagnosis—Dorsum without stripes, color pale yellow to white; caudal metatergal margins indistinctly upturned, caudolateral corners of midbody metatergites slightly but distinctly extended and rounded; telson broad, comprising entire breadth of caudal extremity; sternal lobes of anterior gonopods relatively long, widely segregated; coxal lobe of latter long and narrow, apically rounded, leaning laterad and overlapping 4th and 5th podomeres; dorsal branch of ultimate podomere short and broad, apically blunt, curved slightly ventrad and directed submediad; ventral lobe of ultimate podomere distinct, clearly overhanging dorsal branch; ultimate podomere of posterior gonopod apically fimbriate (Figs. 16-18).

Table 3. Segment Numbers and Average Lengths (mm) of *O. prolata* (no. individuals averaged in parentheses).

County	Locality	Males		Females	
		Segs.	Lengths	Segs.	Lengths
Douglas, OR	Canyonville	34	6.8	(2) 34	7.3
		30	5.6	31	6.8
		(2) 24	3.8		
Douglas, OR	2 mi E Canyonville	38	9.2	32	7.2
		36	8.4		
		31	6.0		
		30	5.4		
Josephine, OR	SW Wolf Creek	45	9.2		
Josephine, OR	1 mi S O'Brien			30	5.6
Josephine, OR	2.5 mi S O'Brien	35	7.9		
Jackson, OR	6 mi S Ruch	32	6.6	37	8.5
		29	6.9	31	6.2
		27	5.7	26	6.3
		25	4.8	21	5.0
		(2) 23	4.2		
		22	4.2		

Variation—Males with seemingly mature gonopods have from 22 to 38 segments and vary in length from 4.2 to 9.2 mm. Female segment numbers vary from 21 to 37 and lengths, from 5.0 to 8.5 mm. These data are presented in table 3, with localities arranged in a general, north to south, sequence; no geographic trends are evident.

Ecology—The types were retrieved from alder litter and moss, wood, and soil; another sample was discovered under “rotten madrone wood.”

Distribution—A small subtriangular area in southwestern Oregon, slightly to the east of the northern range periphery of *O. bivirgata* (Fig. 28); dimensions are about 63 mi (100.8 km), north/south, and 35 mi (56 km), east/west. In addition to the types, specimens were examined as follows:

OREGON: *Jackson Co.*, 6 mi (9.6 km) S Ruch, 7M, 4F, 13 November 1971, EMB (WAS). *Josephine Co.*, along Grave Cr., SW Wolf Creek (town), M, 30 May 1952, V. Roth (FSCA); 1 mi (1.6 km) S, 0.5 mi (0.8 km) W O'Brien, F, 18 December 1971, EMB (WAS); and 2.5 mi (4 km) S, 1 mi (1.6 km) W O'Brien, M, 18 December 1971, EMB (WAS).

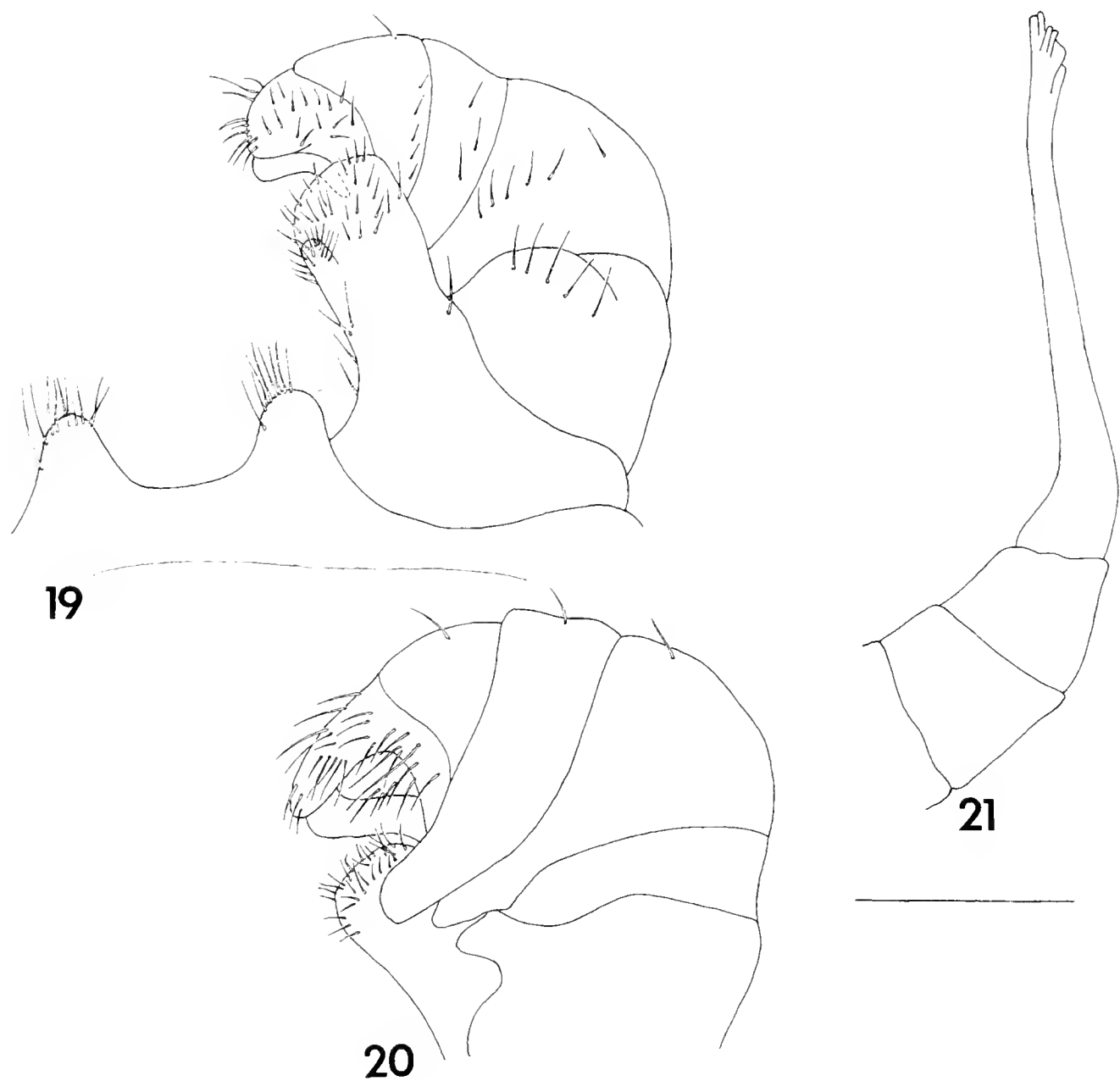
Octoglena sierra, new species

Figs. 19-21

Type specimens—Male holotype and one male and one female paratypes (VMNH) collected by Smith and R. O. Schuster, 15 April 1958, 4 mi (6.4 km) W Newcastle, Placer County, California; other paratypes from this locality include 5 males and 3 females (VMNH) by same collectors, 12 March 1958; one male (NCSM) by same collectors, 10 March 1959; and 2 females (VMNH) by Lange, Smith, and R. O. Schuster, 21 March 1958; one female paratype (VMNH) by Smith and R. O. Schuster, 19 March 1959, 4 mi (6.4 km) N Newcastle.

Diagnosis—Dorsum without stripes, color pale yellow to white; caudal metatergal margins strongly upturned, caudolateral corners of midbody metatergites slightly but distinctly extended and rounded; telson broad, comprising entire breadth of caudal extremity; sternal lobes of anterior gonopods relatively short, widely segregated; coxal lobe of latter long and relatively broad, leaning mediad, overlapping 4th-6th podomeres; dorsal branch of ultimate podomere long, narrow, and sinuate, apically acuminate, directed sublaterad; ventral lobe of ultimate podomere short and indistinct, only slightly overhanging dorsal branch; ultimate podomere of posterior gonopod apically fimbriate (Figs. 19-21).

Variation—Males with seemingly mature gonopods have from



Figs. 19-21. *O. sierra*, holotype. 19, right anterior gonopod and sternum, anterior view. 20, left anterior gonopod, caudal view. 21, distal podomeres of right posterior gonopod, caudal view. Scale line = 0.25 mm for all figs.

Table 4. Segment Numbers and Average Lengths (mm) of *O. sierra* (samples at one locality are combined; no. individuals averaged in parentheses)

County	Locality	Males		Females	
		Segs.	Lengths	Segs.	Lengths
Placer, CA	4 mi W Newcastle	(2) 49	11.7	41	11.9
		42	9.3	39	11.0
		38	9.0	38	9.8
		36	7.1		
		(3) 35	7.2		
		34	7.8		
Placer, CA	4 mi N Newcastle			43	11.5

34 to 49 segments and vary in length from 7.1 to 11.7 mm, the shortest individual having 36 segments and being 0.7 mm shorter than that with the least segments. Female segment numbers vary from 38 to 43 and lengths, from 9.8 to 11.9, the latter, of an individual with 41 segments, being 0.4 mm longer than the female with the most segments (table 4).

Ecology—One paratype sample was encountered in “litter under oak.”

Distribution—A localized species known only from the type and paratype localities in the foothills of the Sierra Nevada (Fig. 28), *O. sierra* is detached from the coastal representatives and occurs some 75 mi (120 km) east of the nearest site of *O. bivirgata*, in Colusa County. It is the easternmost western species and occupies an intermediate geographical position, albeit far to the western side of the generic range. By combining gonopodal attributes of *O. gracilipes*, the long, sinuate dorsal branch and the indistinct ventral lobe, with a trait of the coastal species, the coxal lobe, *O. sierra* links the anatomical extremes, which justifies congeneric status.

Octoglena gracilipes (Loomis), new combination

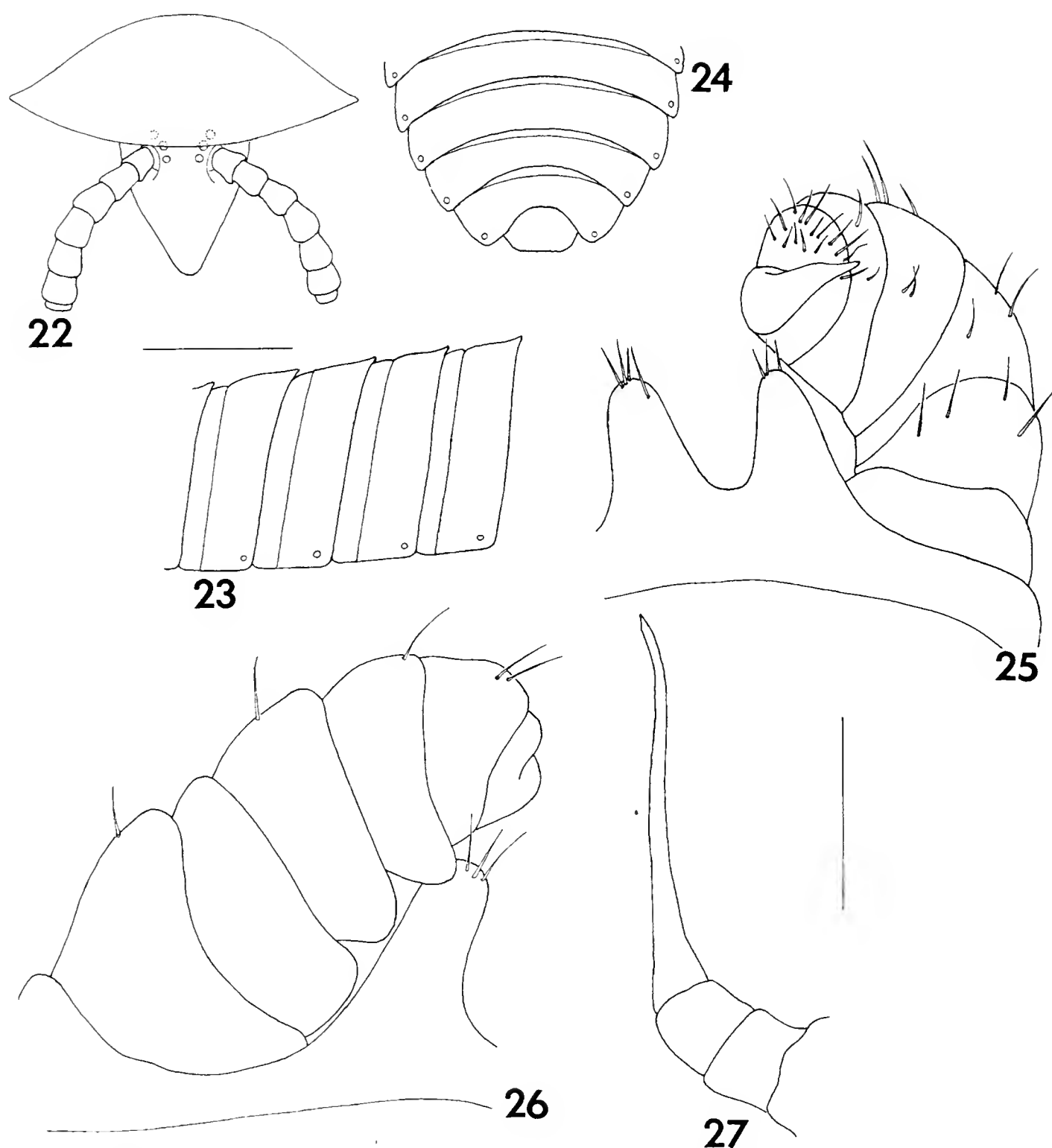
Figs. 22-27

Polyzonium gracilipes Loomis, 1971:157-159, figs. 18-23.

Type specimens—Male holotype and one male and one female paratypes (NMNH) and one male and one female paratypes (FSCA) collected by H. R. Steeves, 17 June 1962, at Cloudland Canyon State Park, Dade County, Georgia. The NMNH sample also includes one male and three female polyzoniids.

Diagnosis—Dorsum without stripes, color pale yellow to white; caudal metatergal margins moderately upturned, caudolateral corners of midbody metatergites not extended, contiguous with middorsal margins, blunt; telson narrow, comprising about half of breadth of caudal extremity; sternal lobes of anterior gonopods relatively long, narrowly segregated; coxae of latter without lobes; dorsal branch of ultimate podomere long, narrow, and sinuate, apically acuminate, directed sublaterad; ventral lobe of ultimate podomere indistinct, not overhanging dorsal branch; ultimate podomere of posterior gonopod apically narrow and attenuated (Figs. 22-27).

Variation—Measurable males with seemingly mature gonopods have from 19 to 33 segments and vary in length from 2.8 to 7.9 mm; female segment numbers vary from 13 to 35, while lengths vary from 1.7 to 8.5 mm. These data are presented in table 5 with localities arranged in a general east to west sequence. Lengths appear roughly



Figs. 22-27. *O. gracilipes*, holotype. 22, head and collum, anterior view, setation omitted. 23, midbody segments, lateral view of left side. 24, telson and caudal tergites, dorsal view. 25, right anterior gonopod and sternum, anterior view. 26, the same, caudal view. 27, distal podomeres of left posterior gonopod, caudal view. Upper scale line = 0.50 mm for figs. 22-24; lower line = 0.25 mm for figs. 25-27.

comparable throughout the range, and no geographic trends are evident.

Ecology—Habitat notations on vial labels include “virgin cove forest,” “under logs,” and “wooded hillside.” Specimens from Cleburne County, Alabama, and Greenwood County, South Carolina, were encountered in ravines.

Distribution—The Piedmont Plateau, Blue Ridge, Ridge and Valley, and eastern Cumberland Plateau Physiographic Provinces of Tennessee,

Table 5. Segment Numbers and Average Lengths (mm) of *O. gracilipes* (samples at one locality combined; lengths averaged for individuals with same segment number, n in parentheses).

County	Locality	Males		Females	
		Segs.	Lengths	Segs.	Lengths
Chester, SC	13.6 mi W Chester			30	8.2
Greenwood, SC	Ware Shoals			28	7.9
Polk, NC	Saluda			25	4.8
Transylvania, NC	SE L. Toxaway	33	7.9		
Macon, NC	Ellicott Rock	19	2.8	22	4.1
				19	2.8
Macon, NC	3.6 mi E Highlands	20	3.5	19	2.6
				(2) 18	2.5
				16	2.0
				15	2.2
				13	1.9
Rabun, GA	E of Satolah			28	7.7
Graham, NC	6 mi SE	31	7.6	32	8.6
	Beech Gap	30	6.3		
Graham, NC	Kilmer Mem. For.	27	5.8		
Sevier, TN	1.4 mi N Gatlinburg			28	7.7
Cumberland, TN	Ozone			30	6.7
				29	7.3
				21	3.5
Dade, GA	Cloudland Cyn. St. Pk.			31	7.3
				30	6.7
				27	6.0
Jackson, AL	Princeton			23	4.6
Cleburne, AL	N of Heflin	26	4.4	25	5.1

Table 5. Continued.

County	Locality	Males		Females	
		Segs.	Lengths	Segs.	Lengths
Clay, AL	Talladega Nat For.			28	6.4
Franklin, AL	The Dismals			35	8.5
				20	2.9
				15	1.7

North and South Carolina, Georgia, and Alabama (Fig. 29), some 1,897 mi (3,035 km) east of the most proximate western species, *O. sierra*. The area is oriented generally east to west, extends from westcentral South Carolina to southcentral Tennessee and northwestern Alabama, and covers approximately 220 mi (352 km), north/south, and 380 mi (608 km), east/west. Specimens were examined from the following localities:

SOUTH CAROLINA: *Chester Co.*, 13.6 mi (21.8 km) W Chester, Woods Ferry Rec. Area, Sumter Nat. For., along USFS rd. 574, 3 mi (4.8 km) W jct. SC hwy. 49, F, 4 August 1976, R. M. Shelley (NCSM). *Greenwood Co.*, Ware Shoals, F, 29 May 1960, L. Hubricht (VMNH). *Oconee Co.*, along SC hwy. 28, exact site unknown, F, 29 July 1960, collector unknown (AMNH).

NORTH CAROLINA: *Graham Co.*, Joyce Kilmer Mem. For., M, 20 May 1970, W. A. Shear (WAS); 6 mi (9.6 km) SE Beech Gap, 2M, F, May 1958, L. Hubricht (VMNH); and Stratton Gap, 2F, 27 May 1959, L. Hubricht (VMNH). *Jackson Co.*, Whiteside Cove, F, 26 July 1958, R. L. Hoffman (VMNH). *Macon Co.*, Highlands, Highlands Biol. Sta., M, 10 August 1955, P. J. Darlington (VMNH); 3.6 mi (5.8 km) E Highlands, Horse Cr. Clearcut, M, 6F, 16 June 1976, F. A. Coyle (NCSM); and 7.5 mi (12 km) SSE Highlands, along Bull Pen Rd. nr. Ellicott Rock, M, 2F, 6 July 1976, F. A. Coyle (NCSM). *Polk Co.*, Saluda, 2F, 5 August 1910, collector unknown (FSCA). *Transylvania Co.*, Thompson R. Gorge SE L. Toxaway, M, 5 September 1961, R. L. Hoffman (VMNH).

GEORGIA: *Dade Co.*, Cloudland Cyn. St. Pk., 3M, 2F, 17 June 1962, H. R. Steeves (FSCA, NMNH) and 3F, 16 May 1972, S. Peck (WAS) TYPE LOCALITY. *Rabun Co.*, along Glade Mtn. Rd. E of Satolah, F, 6-8 September 1961, R. L. Hoffman (VMNH).

TENNESSEE: *Cumberland Co.*, Ozone, below Ozone Falls, 5F, 21 May 1961, L. Hubricht (VMNH). *Sevier Co.*, 1.4 mi (2.2 km) N Gatlinburg, F, 17 May 1961, L. Hubricht (VMNH).

ALABAMA: *Clay Co.*, Talladega Nat. For., exact site unknown, F, 16 April 1960, H. R. Steeves (FSCA). *Cleburne Co.*, ravine nr. Skyway N of Heflin, 2.4 mi (3.8 km) N Bankhead Fire Tower, 2F, 23 October 1960, L. Hubricht (VMNH). *Franklin Co.*, "The Dismals," ca. 13 mi (20.8 km) SSW Russellville, M, F, 18 July 1959, 2F, 28 May 1960, and 2M, F, 17 June 1961, H. R. Steeves (FSCA). *Jackson Co.*, Princeton, F, 29 October 1966, H. R. Steeves (FSCA). *Winston Co.*, nr. Natural Bridge Cave, ca. 9 mi (14.4 km) S Haleyville, 2M, F, collector unknown (FSCA).

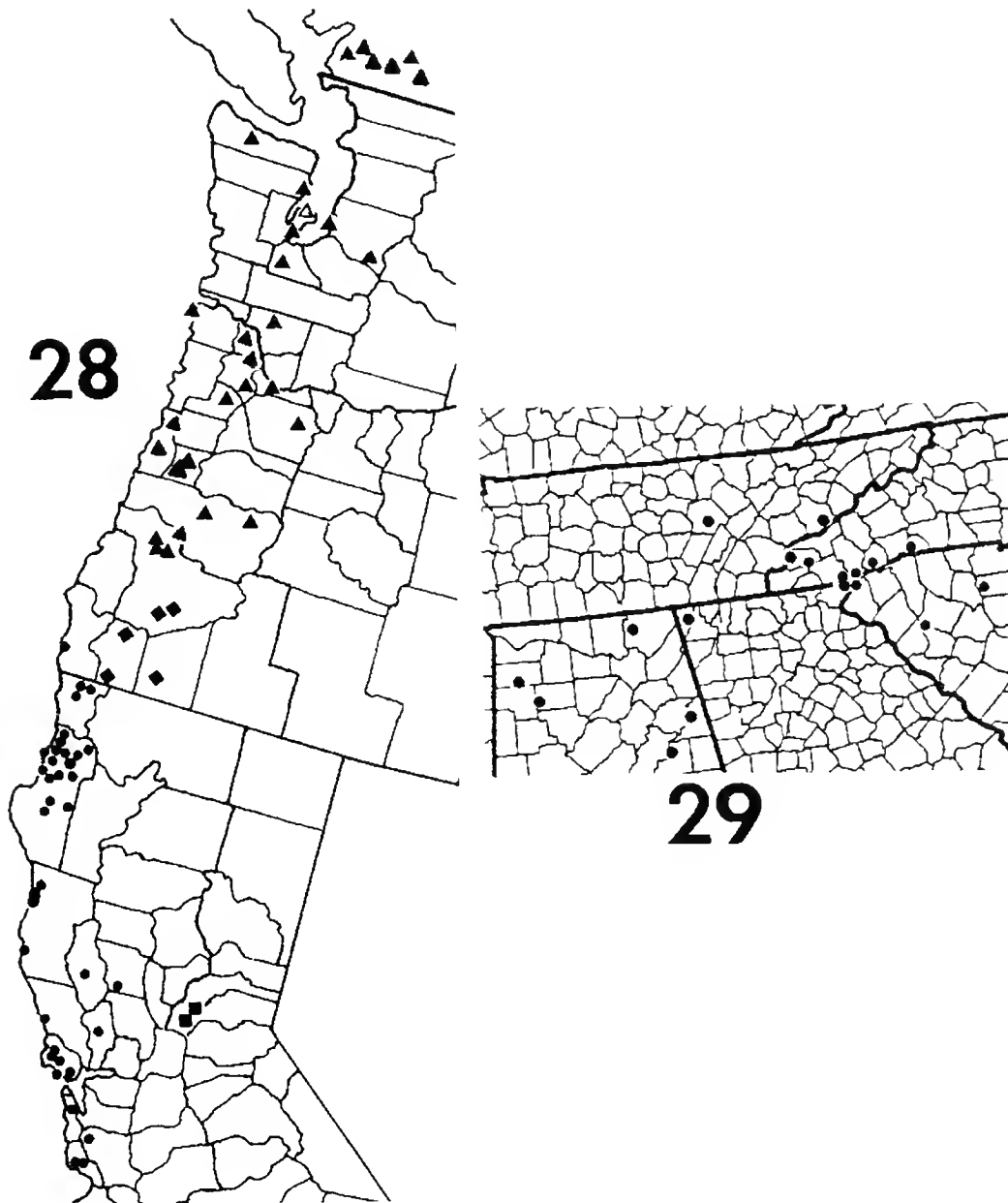


Fig. 28. Distributions of the west-Nearctic Hirudisomatidae. Dots, *O. bivirgata*; triangles, *O. anura*; diamonds, *O. prolata*; squares, *O. sierra*. The open triangle denotes the literature record of *O. anura* from Bremerton, Washington (Chamberlin 1911).

Fig. 29. Distributions of *O. gracilipes* and the Hirudisomatidae in eastern North America.

Although *O. gracilipes* was officially named and described by Loomis (1971), its existence was first mentioned by Hoffman (1969), who called it an undescribed and possibly relictual representative of the Hirudisomatidae in the high mountains of North Carolina, Georgia, and Tennessee.

Mexiconium, new genus

Type species—*Mexiconium absidatum*, new species.

Diagnosis. Dorsum smooth and glossy, polished, with broad, dark middorsal stripe arising on collum and terminating on penultimate segment; body narrow (W/L ratio 16.7%) and vaulted in profile, sides not extending laterad; metaterga with caudal margins slightly elevated but not upturned; collum moderately broad, over-hanging epicranium and part of one pair of ocelli; telson broad, comprising entire breadth of caudal extremity; sternum of anterior gonopods with strong, sparsely hirsute lobes, widely separated from each other; anterior gonopod curving strongly anteriad distad, ultimate podomere with lightly hirsute lobe ventral to and overhanging glabrous dorsal branch, latter long, narrow, and acuminate, extending nearly directly laterad; corners of 4th and 5th podomeres slightly extended on caudal side, latter expanding distad and subuncinate; coxa with broad, glabrous lobe on anterior side, apically rounded; posterior gonopod with ultimate podomere simple and acicular, apically trifurcate.

Species—One is known; others may exist in remote pockets in the Sierra Madre Oriental.

Distribution—Known only from the type locality of the one component species in Vera Cruz, Mexico.

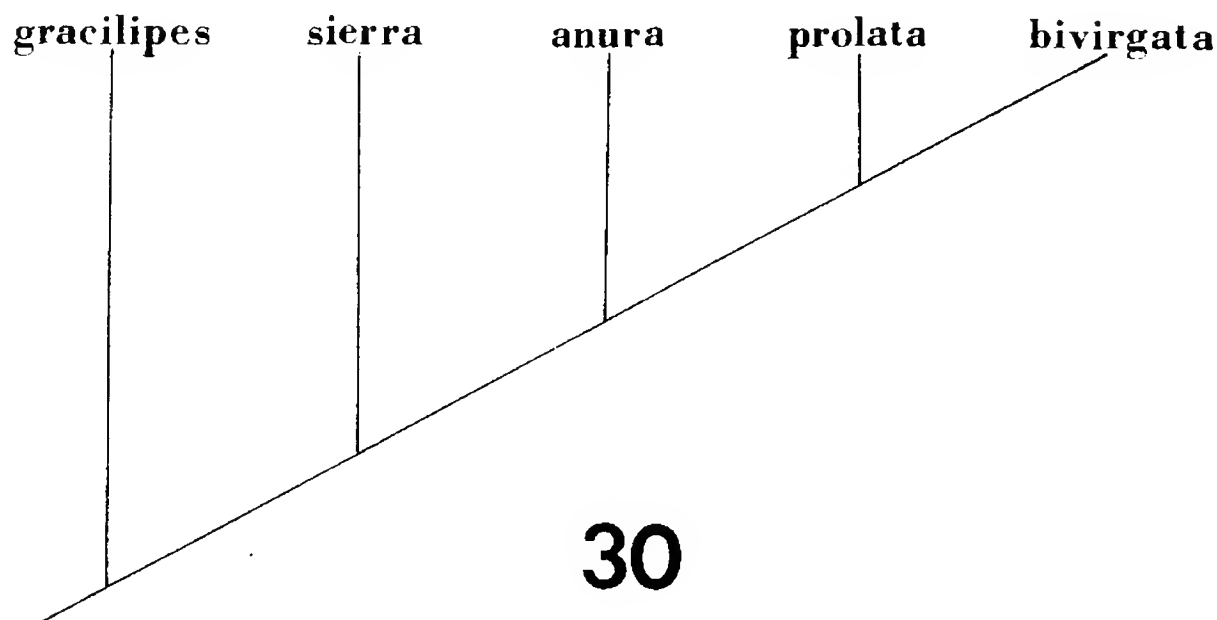


Fig. 30. Relationships in *Octoglena*.

Mexiconium absidatum, new species

Figs. 4, 31-38

Type specimens—Male holotype and two male paratypes (VMNH) collected by R. E. Leech, 25 August 1967, 13.3 mi (21.8 km) S La Vigas [ca. 18 mi (28.8 km) WSW Jalapa], on the north side of Cofre de Perote, Tembladera, Vera Cruz, Mexico.

Diagnosis—With the characters of the genus (Figs. 31-38).

Variation—The holotype has 27 segments and is 6.7 mm long; the paratypes have 29 and 35 segments and measure 7.7 and 10.8 mm, respectively.

Ecology—According to the vial label, the types were collected between 11,500 and 13,500 ft., an extremely high elevation for a North American milliped. The habitat is not indicated.

Distribution—Known only from the type locality, in the Sierra Madre Oriental in the interior of Vera Cruz (Fig. 1), some 440 mi (704 km) south of the Rio Grande and the United States border and around 1,200 and 2,117 mi (1,920 and 3,387 km) from the most proximate sites of *O. gracilipes* and *O. bivirgata*, respectively.

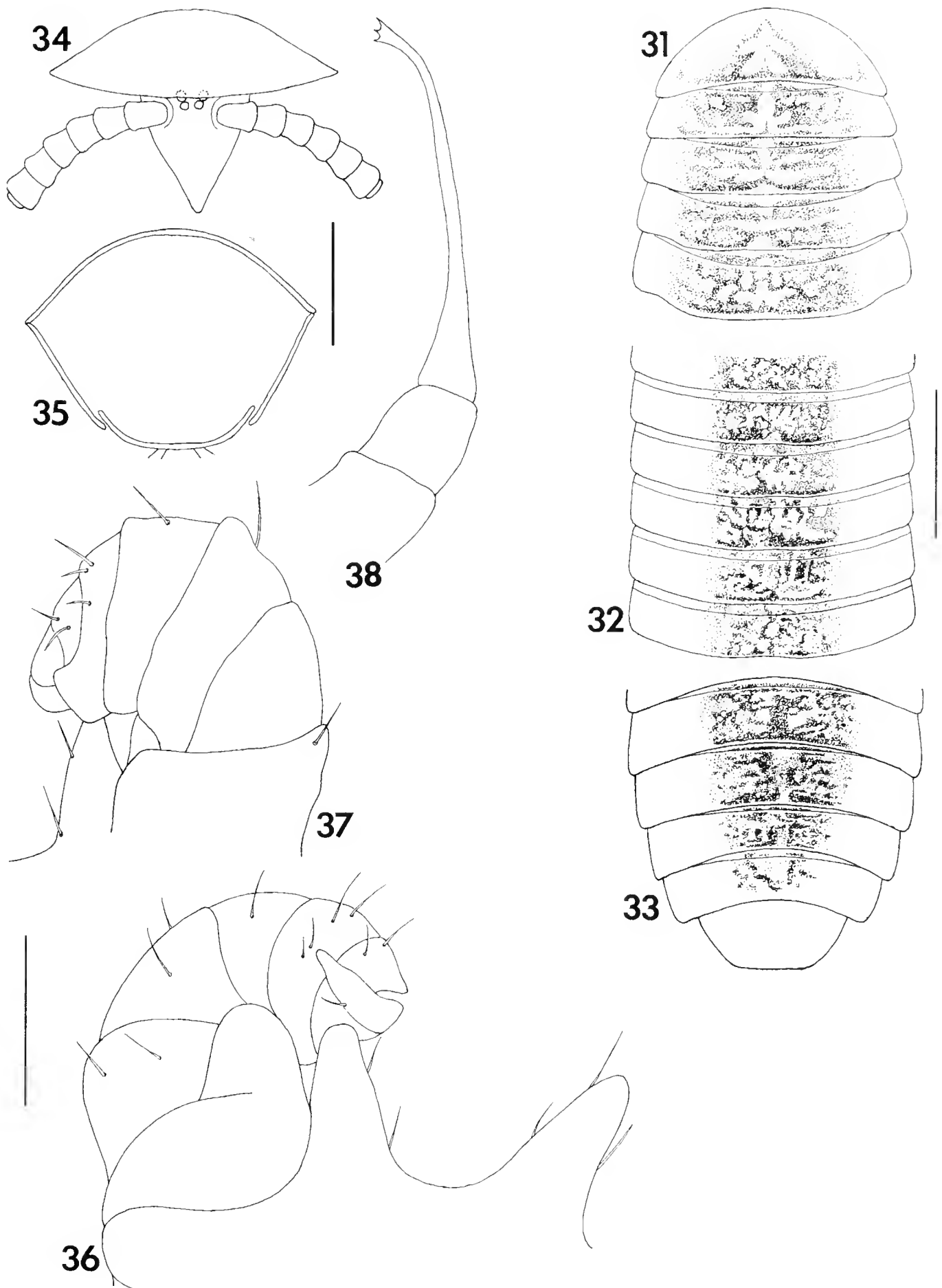
Remarks—This species, the first record of the family from Mexico, is isolated from an ancient dispersal of the Hirudisomatidae across North America that extended southward for an unknown distance into Mexico. The dorsal branch of its ultimate anterior gonopod podomere is similar to those of *O. gracilipes/sierra*, instead of the Pacific Coastal species, and this is further evidence that the Hirudisomatidae dispersed from east to west across North America, as is its occurrence on the eastern side of Mexico rather than the west (see below). The specific name refers to the vaulted body form.

Discussion

The two great allopatries in the Hirudisomatidae merit elaboration because they exemplify broader patterns among Nearctic Diplopoda. The family's occurrence in Mexico is evidence of southward expansion of ancestral stock, a dispersal also demonstrated by the Glomeridae, Spirobolidae, Parajulidae, Nearctodesmidae, and Xystodesmidae. The Mexican xystodesmid fauna exhibits Appalachian affinities and also immigrated from the east-Nearctic (Hoffman 1969), but the austral representatives of the other families have west-Nearctic relationships and occur more in western Mexico, aside from cave inhabiting species of *Glomeroides* Chamberlin (Glomeridae) in Nuevo Leòn, Tamaulipas, and Vera Cruz. Like the Hirudisomatidae, the species of the Spirobolidae, Parajulidae, and Nearctodesmidae show further evidence of Nearctic ancestry in their occurrences at high elevations, in "Nearctic" environments,

Table 6. Disjunctions between Mexico/south Texas and the eastern and western United States

Taxon	Proximate Localities	Breadths of Lacunae
Hirudisomatidae <i>Mexiconium/Octoglena</i>	W of Jalapa, Vera Cruz, Mexico Santa Cruz Co., CA/Franklin Co., AL	2,117 mi (3,387 km), Mex.- CA 1,200 mi (1,920 km), Mex.- AL
Xystodesmidae <i>Rhysodesmus/Boraria</i>	Willacy Co., TX Ouachita Co., LA	560 mi (896 km)
Nearctodesmidae <i>Sakophallus/Nearctodesmus</i>	Volcan de Colima, Jalisco, Mexico Marin Co., CA	1,682 mi (2,691 km)
<i>Glomeroides</i> <i>G. patei/G. prima</i>	Cuautemoc, Neuvo Leòn, Mexico Contra Costa Co., CA	1,460 mi (2,336 km)



Figs. 31-38. *M. absidatum*, holotype. 31-33, pigmentation patterns of anterior, midbody, and caudal segments, respectively. 34, head and collum, anterior view, setation and pigmentation omitted. 35, profile of midbody segment, caudal view. 36, left anterior gonopod and sternum, anterior view. 37, the same, caudal view. 38, left posterior gonopod, caudal view. Scale line for figs. 31-33 = 1.00 mm for each; line for figs. 34-35 = 0.50 mm for each; line for figs. 36-38 = 0.25 mm for each.

at sites that are latitudinally in the Neotropics or the transition zone between the two biogeographic regions. In the Parajulidae, Causey (1974) reported that Mexican forms occur in the temperate zone near the coast but are absent from the "tierra caliente" lowlands; they are most abundant on the plateau and follow the mountains southward into western Guatemala, where they are restricted to the mountains. Likewise in the Spirobolidae, *Hiltonius* Chamberlin extends southward from southern Arizona to southwestern Guatemala, where forms occur only "in high mountainous regions" (Keeton 1960). Finally, *Sakophallus simplex* Chamberlin, a species with west-Nearctic affinities provisionally assigned to the Nearctodesmidae, is known only from high elevations in western Jalisco and Michoacan (Shelley 1994a).

The Xystodesmidae, Nearctodesmidae, and Glomeridae also exhibit substantial Mexico/United States range disjunctions (Table 6). The degree of continuity is unknown in the Parajulidae, which has never been comprehensively studied at the generic and specific levels, and although Keeton (1960) revised *Hiltonius*, enough new material exists in American repositories to reassess the Mexican forms, which range northward into Santa Cruz County and adjacent parts of southern Arizona. A hiatus appears to exist between southern Arizona and coastal California, and there may or may not be one in Mexico. The Mexican representatives of the Xystodesmidae, *Rhysodesmus* Cook and *Stenodesmus* Saussure, also occur in the adjacent fringe of the United States, and there is a sizeable lacuna between them and the east-Nearctic species, the most proximate localities being in the lower Rio Grande Valley of Texas and northern Louisiana (Hoffman and Shear 1964, Hoffman 1970, Shelley 1987).¹ An even larger gap exists between the most proximate sites of *Sakophallus* Chamberlin, in Jalisco, and *Nearctodesmus* Silvestri, in Marin County, California (Shelley 1994a). Regarding *Glomeroides*, the only United States species, *G. prima* (Silvestri), occurs in the San Francisco Bay area. The type locality is in Marin County; Shear (1986) reported Pfeiffer Big Sur State Park, Monterey County; and I now add Redwood Regional Park, Contra Costa/Alameda counties, based on juveniles collected on 18 May 1953 by R. O. Schuster and E. E. Gilbert (NMNH).

¹ The Louisiana species is *Boraria profuga* (Causey), known previously only from the type locality in Montgomery County, Arkansas, in the Ozark-Ouachita Physiographic Province. The Louisiana locality, in the Gulf Coastal Plain, is Monroe, Ouachita County, based on unreported males and females collected in December 1974 and 1978 by M. R. Cooper (NCSM).

Table 7. Generic and Tribal, East/West Nearctic Disjunctions.

Taxon	No. Components		Proximate Localities (County, State)	Breadths of Lacunae	Probable Dispersal Directions
	West	East			
<i>Octoglena</i>	4 spp.	1 sp.	Placer, CA Franklin, AL	1,897 mi 3,035 km	E→W
<i>Brachygybe</i>	3 spp.	2 spp.	Placer, CA Benton, AR	1,485 mi 2,376 km	unknown
<i>Orinisobates</i>	2 spp.	1 sp.	Summit, UT Johnson, IL	1,192 mi 1,907 km	W→E
<i>Ergodesmus</i>	1 sp.	1 sp.	Lewis & Clark, MT Pike, IL	1,150 mi 1,840 km	W→E
Chonaphini	5 gen. 11 spp.	1 gen. 1 sp.	Missoula, MT Rice, MN	1,060 mi 1,696 km	W→E
<i>Scytonotus</i>	6 spp.	3 spp.*	Sublette, WY Shawnee, KS	984 mi 1,574 km	W→E

*One eastern species is widespread; the others are Appalachian endemics and reflect a secondary center of evolution in the southern Blue Ridge Province (Shelley 1993).

The east/west allopatry in the United States is a consistent pattern among Nearctic Diplopoda, not only in the disjunction, but also in the greater western diversity. *Scytonotus*, *Orinisobates*, *Brachygybe*, and *Octoglena* have more western than eastern species, as does the transcontinental xystodesmid tribe Chonaphini, with five western genera and eleven species, versus one of each in the east (Table 7) (Gardner 1975, Enghoff 1985, Shelley 1993, 1994b). *Ergodesmus* is an exception, but the western species occupies a much larger area and demonstrates more variation (intraspecific diversity) than the eastern species, which comprises small populations and is restricted to caves in Illinois (Shelley 1994a). Western origins have been postulated for *Scytonotus* and the Chonaphini (Shelley 1993, 1994b), and Enghoff (1985) concluded that *Orinisobates* probably arose in the eastern Palearctic and invaded the Nearctic via the Bering Bridge, so it too probably spread from west to east across North America. Consequently, the east-Nearctic components of these taxa appear to represent the results of range expansions, rather

than remnants that remained in the original source area. *Octoglena* conforms to this diversity pattern, but the eastern component is sister to the western species, implying dispersal from east to west. The overall distribution of the family, with the greatest diversity in Europe, supports this scenario and suggests a Laurasian origin for the New World fauna. Furthermore, the continuous, parapatric ranges and the absence of extinctions along the Pacific Coast contrast so strongly with the allopatries and lacunae elsewhere in the New World that they probably reflect recent evolution and the end products of range expansion. *Octoglena* therefore represents the northern part of an Ancient Holarctic faunal assemblage that probably spread from east to west across the United States, and southward into Mexico, in one or possibly two dispersals. There has been considerable extinction, as evidenced by the extensive lacunae; that between *O. sierra* and *O. gracilipes* is greater than those in other disjunct taxa in the United States (Table 7), and coupled with the unique somatic features of *O. gracilipes*, implies lengthy isolation of the eastern and western hirudisomatid faunas.

Hoffman (1969) cited three distribution patterns that have impacted Appalachian Diplopoda -- Ancient Holarctic, Tertiary Nearctic Endemism, and Late Coenozoic Austral Immigration. These also affected lowland areas, and "West-Nearctic Immigration", from beyond the Continental Divide, seems equally important in understanding the origins of the fauna east of the Plains. Causey (1974) postulated a west-Nearctic origin for the Parajulidae, with dispersal centers in central California and around Puget Sound that gave rise to the east-Nearctic and Mexican/Guatemalan faunas. This hypothesis is consistent with the conclusion of Shelley (1994c) that the exclusively western julidan superfamily Paeromopodoidea probably arose from a parajuloid-like ancestor along what is now the border between Oregon and California. This is a key area in the evolution of west-Nearctic diplopods (Shelley 1994c), being the apparent primary centers of evolution of the Paeromopodoidea and *Scytonotus*, and harboring a peripheral relict species of *Chonaphe* Cook (Shelley 1993, 1994b, c). The area also seems to be a secondary center of evolution within *Octoglena*, thereby accounting for the greater diversity, parapatry, and abundance of the Pacific Coastal components.

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